The Chondrocranium of Calotes versicolor (Daud.) with a Description of the Osteocranium of a just-hatched Young

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With 16 Text-figures

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INTRODUCTION

THE chondrocranium of a number of lizards has been described, viz. Lacerta (Leydig, 1872; Parker, 1880; Gaupp, 1900, 1906; de Beer, 1930); Ascalabotes (Sewertzoff, 1900); Hemidactylus, Platydactylus (Versluys, 1903); Anguis (Zimmermann, 1913); Eumeces (Rice, 1920); Lygosoma (Pearson, 1921); Platydactylus (Hafferl, 1921); Lygodactylus, Pachydactylus, and Agama (Brock, 1932); Ablepharus (Haas, 1935). In the descriptions of the adult skull of Chalcides (Haas, 1936) and Acontias (de Villiers, 1939) persistence of chondrocranial cartilages in various regions is also noticed. Boulenger (1890) gives figures of lateral, dorsal, and ventral aspects of the adult skull of Calotes jubatus (Dum and Bibr.) which are also reproduced in the latest edition of "Sauria" in "Fauna of British India" (Smith, 1936). The columella auris has been studied in Lacerta (Hoffmann, 1889; Versluys, 1898, 1903; Cords, 1909; Dombrowsky, 1918, 1924), and the adult hyoid apparatus of Calotes versicolor is described by Gnanamuthu (1937) and Narayanaswamy Iyer (1943).

I propose to describe in detail the fully formed chondrocranium of Calotes versicolor (Daud.) while making references to important points in three earlier stages, and as well the osteocranium of a just-hatched form. The adult skull is described by Narayanaswamy Iyer (1943).

Material and Methods

The following are the stages of Calotes versicolor (Daud.) studied:

Head-length.	3·6 mm.	Embryos.
,,	6·0 mm.	
,,	7·0 mm.	
,,	8·0 mm.	
,,	8·0 mm.	Just-hatched young.

The fully formed chondrocranium described belongs to an embryo of a head-length of 8·0 mm.; the head of the just-hatched lizard also measured the same. Alizarin transparencies of 8·0 mm. embryo and just-hatched young, van Wijhe's preparations of all the stages and wax models of the chondrocranium of the embryonic stages have been made.

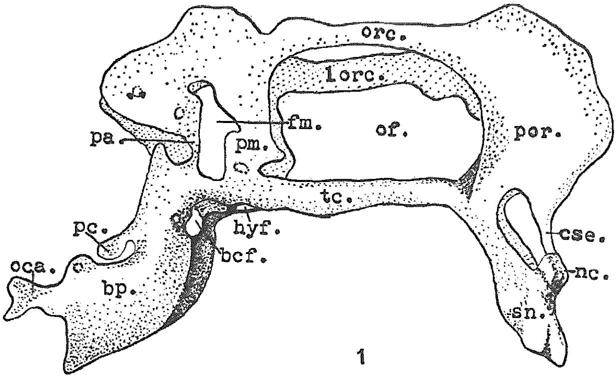
I wish to express my sincere thanks to Professor E. S. Goodrich for having gone through the paper and for helpful criticism, and also to Professor A. Subba Rau for lending Gaupp's paper on Lacerta from his personal library.

Observations

I *a*. Embryo, H.-L. 3·6 mm. (Text-fig. 1).

In the occipital region, the occipital arch (Text-fig. 1, *oca*) arising from the basal plate (*bp*) is unconnected by a tectum.

The otic capsule is not yet formed but for the slight formation of cartilage in the region of the future recessus scalae tympani lateralis (metotic fissure). The independent cochlear cartilage (*pc*) is united with the basal plate by a basicochlear commissure; while on one side a prefacial commissure is noticed, on the other the facial root is unenclosed. The basal plate shows one hypoglossal foramen on one side and two on the other.



TEXT-FIG. 1.

The chondrocranium of a 3·6-mm. (H.-L.) embryo of Calotes versicolor (Daud.), ×50 (model). *bcf*, basicranial fenestra; *bp*, basal plate; *cse*, commissura sphenoethmoidalis; *fm*, fenestra metoptica; *hyf*, hypophysial fenestra; *lorc*, left orbital cartilage; *nc*, cartilage of nasal capsule; *oca*, occipital arch; *of*, optic fenestra; *orc*, right orbital cartilage; *pa*, pila antotica; *pc*, prominentia cochlearis; *pm*, pila metoptica; *por*, preoptic root; *sn*, septum nasi; *tc*, trabecula communis.

There is an interesting feature in the condylar region. The notochord is dorsal to the basal plate. The occipital arch is united with the basal plate and represents the neural arch (*bd*) of the proatlas vertebra; the hypocentrum (*bv*) of this fuses with the basal plate to form the single condyle. Normally this must fuse with the pleurocentrum (*id*) behind it to form a vertebra. However, in lacertilians, in the condylar region this pleurocentrum fuses instead with the pleurocentrum of the atlas and both with the same of the axis vertebra which forms the odontoid process. That the occipital condyle is formed by the hypocentrum of the proatlas, which at least is temporarily united with its own pleurocentrum, is seen in this stage of Calotes (Text-fig. 15 F). Here the fusion is seen between the basal plate (inclusive of the hypocentrum of the proatlas vertebra), the pleurocentrum of proatlas and atlas vertebrae and that of the axis. A similar phenomenon has been described in Eumeces, where Rice (1920) recorded the confluence of the cartilage of the odontoid process and the basal plate. The occipito-atlantal joint is, therefore, intravertebral in lacertilians.

In the orbitotemporal region the orbital cartilages (Text-fig. 1, *orc*) are paired and separate. Extending from the posterior region of the pila antotica (*pa*) with which each orbital cartilage is united, it ends anteriorly as a short projection in front of its union with the preoptic root (*por*) and shows a number of fenestrae due to absence of chondrification in the wall. In front of the pila antotica (*pa*) arising from the lateral aspect of the crista sellaris, the pila metoptica (*pm*) of each side unites with the orbital cartilage and between the two pilae there is the metoptic fenestra (*fm*) in which the oculomotor nerve gains exit either through an incomplete or complete orifice in the pila metoptica (*pm*). The trochlear nerve gains exit between the pila antotica and the orbital cartilage, i.e. in the dorsal part of pila metoptica or through an orifice in the orbital cartilage. The abducens nerve passes out anteriorly to the incisura prootica and becomes extracranial in the metoptic region.

The trabecula communis (*tc*) formed anteriorly to the hypophysial fenestra (*hyf*) is continuous with the unfenestrated nasal septum (*sn*); the orbital cartilage widens in the region of the nasal septum and unites with the trabecula by means of the preoptic root (*por*). Further anteriorly, the sphenethmoid commissures (*cse*) unite the orbital cartilages with the nasal capsule (*nc*).

A parietotectal cartilage is feebly represented.

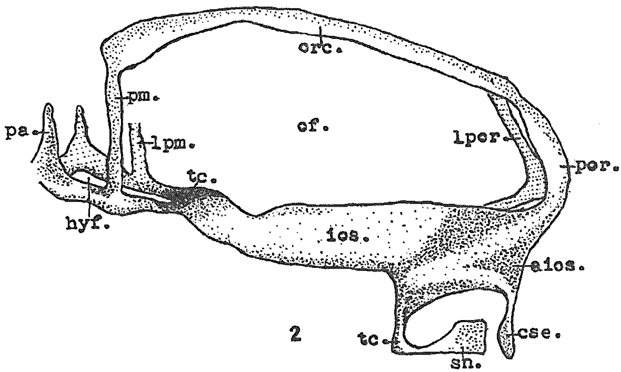
A sclerotic cartilage is formed.

The processus pterygoideus is still in a dense mesenchymatous condition and a processus ascendens is not formed, so also the basitrabecular process; a meniscus pterygoideus is recognizable as a deep mass of mesenchyme.

Meckel's cartilage is well developed, a feature also noticed in other lizards.

I *b*. Embryo, H.-L. 6·0 mm. (Text-fig. 2).

It was not possible to secure stages between the previous and the present.



TEXT-FIG. 2.

The chondrocranium of a 6·0-mm. (H.-L.) embryo of Calotes versicolor (Daud.), ×50 (model); otic capsules and a part of the nasal capsule not included. *aios*, anterior portion of interorbital septum; *cse*, commissura sphenoethmoidalis; *hyf*, hypophysial fenestra; *ios*, interorbital septum; *lpm*, left pila metoptica; *lpor*, left preoptic root; *of*, optic fenestra; *orc*, right orbital cartilage; *pa*, pila antotica; *pm*, right pila metoptica; *por*, right preoptic root; *sn*, septum nasi; *tc*, trabecula communis.

A tectum of the occipito-auditory region is not formed.

The cochlear portion and the semicircular canal cartilages are united by the basicochlear commissure as in the previous stage; a basivestibular commissure is not formed. The fenestra ovalis and basicapsular fenestra are confluent. The foot plate of the columella is seen as an independent mass of cells. Between the posterior semicircular canal portion and the occipital arch, in the fissura metotica, the IX, X, and XI cranial nerves gain exit, while in the basal plate the two hypoglossal foramina are seen. A prefacial commissure is also noticed.

In the orbitotemporal region, the oculomotor and trochlear nerves gain exit through the metoptic fenestra; the abducens cuts the base of the pila antotica and passes through a tunnel in the basal plate for a short distance. The crista sellaris unites the parachordals in the region posterior to the hypophysial fenestra.

An interorbital septum (Text-fig. 2, *ios*) has appeared which posteriorly is continuous with the trabecula communis (*tc*) in front of the hypophysial fenestra (*hyf*). Anteriorly the septum forks and from the dorsal ends of the fork start the preoptic roots (*por, lpor*) and each root is met by the orbital cartilage of its side. The olfactory ends of the forks are joined by the sphenethmoid commissures (*cse*). Thus between the preoptic roots and the sphenethmoid commissures, as it were, the anterior portion of the interorbital septum (*aios*) has been added in the dura mater. The pila metoptica (*pm, lpm*) is paired and united with the orbital cartilages (*orc*) as in the previous stage. There is a single large optic fenestra (*of*) between the interorbital septum and orbital cartilages. As in the previous stage, the orbital cartilage does not project posteriorly to the metoptic pillar.

The unchondrified processus pterygoideus is shorter than in the previous stage and the cartilaginous processus ascendens is well developed with a free meniscus pterygoideus on its medial side. A basitrabecular articulation is also developed.

In the nasal region the nasal septum is well formed and dorsally it is united with the parietotectal cartilage. The sphenethmoid commissure unites with the paranasal cartilage posteriorly.

The sphenethmoid commissure must unite with the antorbital cartilage, but since the latter is not clearly demarcated, it is stated that the commissure unites with the paranasal cartilage. Between the paranasal and the parietotectal cartilages in a large gap the lateral nasal branch of the ethmoid nerve gains exit; thus, the epiphaneal foramen is not yet enclosed.

The nasal septum (*sn*), which is not continuous with the interorbital septum (*ios*), shows ventrally a clubbed appearance;

this thickening continues posteriorly and ends where it meets the interorbital septum. In Lacerta (Gaupp, 1900) and Eumeces (Rice, 1920) it is noticed that the trabecula communis continues anteriorly and unites with the base of the nasal septum and could be easily differentiated from the interorbital septum by its rounded appearance. In Calotes, unlike the previous stage, the trabecula communis cannot be differentiated as in Lacerta or Eumeces.

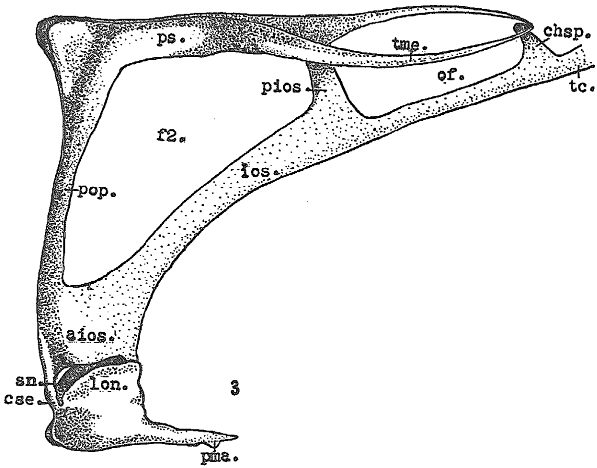
The hyobranchial skeleton is laid down but will be described later (8·0 mm. stage). There is no connexion between the hyoid cornu and the columella.

I *c*. Embryo, H.-L. 7·0 mm. (Text-fig. 3).

The cartilages of the occipital, otic, olfactory, the columella auris and the hyoid apparatus are well formed and will be described in the next stage.

A tectum synoticum plus posterior is noticed in this stage uniting the otic capsules and occipital arches. A short processus anterior tecti is given off from the tectum.

At the region the sphenethmoid commissure (Text-fig. 3, *cse*) unites with the interorbital septum (*ios*), the forked nature of the interorbital septum seen in the previous stage is lost, and the two commissures, therefore, arise from a thick cartilage; from the dorsal end of the septum, the two preoptic roots, which have united together to form a pillar, arise. I have called this the preoptic pillar (*pop*). From the upper end of this pillar is noticed the flooring cartilage for the brain, the planum supraseptale (*ps*) as in Lacerta (Gaupp, 1900) and Eumeces (Rice, 1920). From the posteroventral aspect of the planum the two orbital cartilages, now called taenia medialis (*tme*), proceed posteriorly, and at the region where the taeniae start from the planum, there is an obliquely vertical pillar of cartilage (*pios*). This pillar, not noticed in previous stages, arises from the interorbital septum (*ios*) below, separating an anterior septal fenestra (*f2*) from a posterior optic fenestra (*of*). These paired taeniae mediales (*tme*) unite posteriorly; and slightly in front of this union, the united cartilago hypochiasmatica, subiculum infundibuli and pilae metopticae (*chsp*), arising from the trabecula communis (*tc*) in front of the hypophysial fenestra, unite with the conjoint taeniae. Obviously the taeniae posterior to the united vertical cartilage referred to above represent the reminiscent orbital



TEXT-FIG. 3.

The interorbital septal region of a 7·0-mm. (H.-L.) embryo of Calotes versicolor (Daud.), ×50 (model). *aios*, anterior portion of interorbital septum; *chsp*, pillar formed by the union of cartilago hypochiasmatica, subiculum infundibuli, and pilae metopticae; *cse*, commissura sphenoethmoidalis; *f2*, the larger septal fenestra; *ios*, interorbital septum; *lon*, lamina orbitonasalis; *of*, optic fenestra; *pios*, pillar from the interorbital septum to the posterior portion of planum supraseptale; *pma*, processus maxillaris anterior; *pop*, pillar formed by the fusion of the two preoptic roots; *ps*, planum supraseptale; *sn*, septum nasi; *tc*, trabecula communis; *tme*, taenia medialis.

cartilage which connected the pilae metopticae and antotica in the previous stage.

The incomplete fenestra behind the united vertical cartilage (*chsp*) and in front of the pila antotica represents the metoptic region.

I *d*. Embryo, H.-L. 8·0 mm. (Text-figs. 11–14).

The fully formed chondrocranium belongs to this stage.

1. The Basal Plate and Notochord.

The basicranial fenestra (Text-fig. 2, *bcf*) is noticed, as already described, from the 3·6-mm. stage and is not formed by the resorption of cartilage in this region. The basicapsular and basivestibular commissures are formed (also noted in the previous stage) and the foramen ovalis is limited by the growth of cartilage in the ovalis region of the otic capsule. In the 3·6-mm. stage, the basicapsular fenestra was confluent with the fenestra ovalis. I cannot say when exactly the otic capsule becomes united with the parachordals, not having the stages between 3·6 mm. and 6·0 mm.

From the basicranial fenestra, the basal plate (Text-fig. 11; Text-fig. 12, *bp*) gently rises up towards the foramen magnum (*fma*); anterior to the hypophysial fenestra (Text-fig. 12, *hyf*) the interorbital septum (Text-fig. 11, *ios*) forms a deep arch near the olfactory capsule before uniting with the nasal septum (*sn*). There is a broad prefacial commissure (*pfc*). The pila antotica (Text-figs. 11, 12, *pa*) arises from the anterolateral corner of the basal plate, and in this region the two sides are connected, in front of the basicranial fenestra (Text-fig. 12, *bcf*), by the crista sellaris (*cs*). The abducens nerve pierces the basal plate internally to the pila antotica (*pa*), passes through a tunnel for a short distance, and then emerges in the basal plate by an orifice (*fa*). In the condylar region the notochord (*nc*) runs dorsally in the reniform condyle seen both in 7·0-mm. and 8·0-mm. stages. This condyle is situated between two projections (Text-figs. 11, 12, *oc*) of the basal plate and later the two projections and condyle fuse to give rise to a monocondyle. Even in the adult Calotes, the line of fusion of the hypocentrum between the two exoccipital portions is clearly visible. In Eumeces Rice (1920) described a deep notch between two projecting condyle-like cartilages which he compared with the mammalian bicondyle; in Lacerta (Gaupp, 1900) the two projections are not so prominent.

The notochord in Calotes is wedged in the basal plate except posteriorly, where it runs dorsally; where it enters the odontoid process, it passes through the basal plate for a very short distance. Anteriorly it extends into the basicranial fenestra as far as the crista sellaris (not shown in my figures), as in other lizards.

2. The Occipital Region.

The two principal occipital arches (Text-fig. 11; Text-fig. 12, *oca*) are united dorsally above the foramen magnum (*fma*) by the tectum synoticum (plus tectum posterius) (*tsy*) which also connects the otic capsules. While three preoccipital arches spring from the basal plate on each side in front of the occipital arch enclosing three hypoglossal foramina in Lacerta (Gaupp, 1900), there are only two pairs of hypoglossal foramina (Text-fig. 11, *hy*) in Calotes. Between the otic capsule and the occipital arch there is the jugular foramen (Text-figs. 13 A, 13 B, *fj*) for the exit of the X and XI cranial nerves and jugular vein (corresponding to the posterior portion of the fissura metotica of Lacerta (Gaupp, 1900)). This jugular foramen is practically separated from the more anterodorsal recessus scalae tympani lateralis (*rsl*) by the coming together of the ampullary portion (*ppsc*) of the posterior semicircular canal (*psc*) and the basal plate (*bp*); the connective tissue between these two is so thin that the fissura metotica may be studied in two parts, viz. an anterior recessus scalae tympani lateralis and a posterior jugular foramen. Such a separation is also seen in Lacerta (Gaupp, 1900), while in Eumeces (Rice, 1920) is described an anterior recessus scalae tympani and a posterior foramen jugularis, being formed by the apposition of the posterior ampullary prominence and the basal plate in front of the anterior hypoglossal foramen.

The jugular foramen itself is cut up into a larger anterior (Text-fig. 13 A, *fj*) and a tiny posterior portion (*fj'*) between the occipital arch and the otic capsule, the separation being due to the coming together of otic capsule and the occipital arch. This division is of no significance since no nerves leave the cranium through the posterior orifice. An individual variation of the metotic fissure in Lacerta where it is completely cut into two parts is also noted by Gaupp (1900, Fig. 4).

3. The Auditory Region.

The otic capsules are large and are as long as the basal plate (Text-figs. 13 A, 13 B, *bp*); posteriorly there is the tectum synoticum united with the tectum posterius (Text-fig. 12, *tsy*). From the anterior margin of the tectum, there arises medially a cartilaginous process, the processus anterior tecti (*pat*) supporting the endolymphatic organ. The united basicapsular and basivestibular commissures connect the basal plate with the otic capsule, leaving a large gap for the facial nerve (Text-fig. 11; Text-figs. 13 A, 13 B, *ff*).

External features.—Externally each otic capsule exhibits the following features. The cochlear portion (Text-fig. 13 A, *pc*) is longer than in Lacerta (Gaupp, 1900); and, if a line is drawn connecting the facial foramen (*ff*) to the anterior end of the recessus scalae tympani lateralis (*rsl*), a large portion of the cochlear prominence is cut off as in Eumeces (Rice, 1920). The topography of the remaining parts agrees fairly with that in Lacerta and Eumeces. Laterally the three semicircular canals, viz. the most clearly marked out anterior semicircular canal (*asc*) which is completely separated for a short distance by a gap (*gapc*) from the other two, the prominent posterior semicircular canal (*psc*) separated near the sinus superior (*ss*) by the gap referred to above, and the lateral semicircular canal (*lsc*) forming also a ridge-like prominence, are noticed. Connected with the anterior or inferior openings of these semicircular canals, the ampullary prominences (*pasc, plsc, ppsc*) are also discoverable; the ampullary prominence at the inferior opening of the posterior semicircular canal is not very prominent.

From the prominence of the lateral semicircular canal (*lsc*) is seen a projection, the crista parotica (*cp*), with which another cartilaginous structure, the processus paroticus (*pp*), is continuous. Anteroventrally to these projections, there is the large fenestra vestibuli or ovalis (*fo*) in the cochlear wall. An unchondrified portion (*uc*) in the wall near the processus paroticus is also noticed.

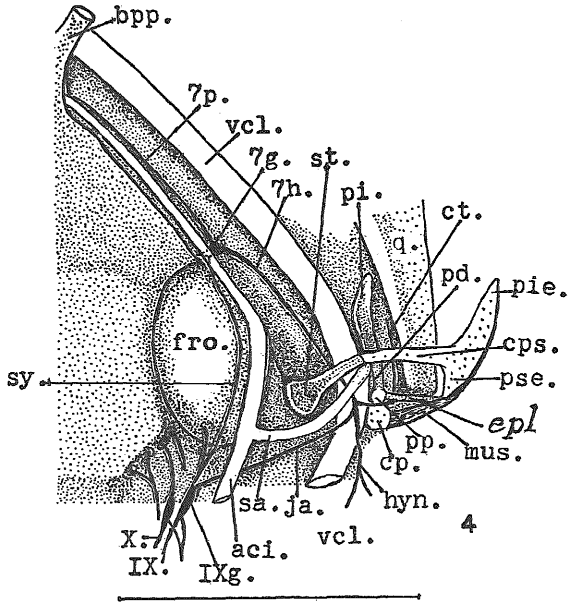
On the medial aspect of the otic capsule (Text-fig. 13 B) a large foramen acusticus anterius (*faa*) and a larger foramen acusticus posterius (*fap*) are noticed. Near the anterior foramen in the basal plate (*bp*) is the facial foramen (*ff*) referred to above. Anterior to this is the prominentia recessus utriculus (*pru*), the wall of which unites with the basal plate forming the prefacial commissure (*pfc*). The endolymphatic foramen (*ef*) is small, unlike that in Eumeces (Rice, 1920), and is posterior to the foramen acusticus posterius. Some unchondrified portions (*uc*) in the form of foramina are also noticed.

The Intracapsular Cavity.—The cavity of the auditory capsule shows the same features as that of Lacerta (Gaupp, 1900) or Eumeces (Rice, 1920). The main cavity is divisible into an anterior smaller cavum vestibulare anterius (Text-fig. 15 A) and a larger posterior cavum vestibulare posterius, the two being separated by a septum intervestibulare (*si*). This septum shows two orifices normally in lizards, viz. a posterior median which permits the utriculus lying in the cavum vestibulare posterius to communicate with the recessus utriculus in the cavum vestibulare anterius and an anterior lateral foramen which is closed by a membrane. In Calotes, however, the median one is not an orifice since it is not limited by cartilage, while the lateral is normal.

The recessus ampullae of the anterior (*raa*) and lateral (*ral*) semicircular canals are at different levels from the utricular recess (*ru*) in the cavum vestibulare anterius and lead into the anterior orifices of the canals respectively (in the figure only one is seen, *aoa*). The roof of the cavum vestibulare anterius is, therefore, formed by the septum semicirculare anterius (*sasc*) till the latter separates itself from the cavum to run dorsally to the gap referred to above (Text-fig. 15 C).

The cavum vestibulare posterius is a spacious chamber into which the cavum cochleare (*cc*) opens anterodorsally. Postero-ventrally, the cavum vestibulare posterius gives rise to the recessus ampullae posterius (*rap*) which continues into the inferior opening of the posterior semicircular canal (Text-fig. 15 C, *ipsc*). The posterior opening (Text-fig. 15 C, *opl*) of the lateral semicircular canal (*lsc*) in the posterior region of the cavum vestibulare posterius is above the posterior ampullary recess near the septum of the posterior semicircular canal (*spsc*). On the posterior aspect of the septum semicirculare posterius (Text-fig. 15 D, *spsc*) the superior orifice of the posterior semicircular canal (*osp*) and the foramen pro sinu superior (*fps*) are noticed. In the recessus sinus superior (Text-fig. 15 E, *rss*) the posterior orifice (*opa*) of the anterior semicircular canal is noticed and in this region the posterior and anterior semicircular canals merge into the sinus superior.

A brief reference may be made to the cartilaginous canals. The three semicircular canals are separated from the cavum vestibulare by septa; the septum of the anterior canal is horizontal (Text-fig. 15 A, *sasc*) and forms the roof of the cavum vestibulare anterius as in Lacerta, but slightly anterior to the region of the posterior opening of the lateral semicircular canal, the otic capsule wall (Text-fig. 15 C, *slsc*) forms the roof of the cavum vestibulare posterius, the membranous anterior semicircular being enclosed in its own canal (*asc*) and thus being separated from the otic capsule by a gap. Posteriorly, however, at the region of the sinus superior, the semicircular canal (Text-fig. 15 E, *asc*) again joins the cavum vestibulare posterius to open into the recessus sinus superior (*rss*). The septum of the lateral semicircular canal (Text-figs. 15 A, 15 B, *slsc*) is obliquely vertical and longitudinal; it partly forms the inner wall of the cavum vestibulare posterius. It anteriorly meets the septum intervestibulare (Text-fig. 15 A, *si*) on the lateral side and projects into the posterior part of the cavum vestibulare anterius. The posterior extension of the septum (Text-fig. 15 C, *slsc*) is seen in the region where the lateral semicircular canal opens into the cavum vestibulare posterius by its posterior orifice (*opl*). The septum of the posterior semicircular canal is short (Text-figs. 15 C, 15 D, *spsc*), vertical and transverse and forms the posterior inner wall of cavum vestibulare posterius. The anterior face of this septum limits the posterior opening of the lateral semicircular canal, while its posterior faces the sinus superior. In this posterior semicircular septum is the foramen pro sinu superior (Text-figs. 15 C, 15 D, *fps*), one edge of which is limited by the otic capsule wall. At the region where the lateral



TEXT-FIG. 4.

The region of the columella auris of a 8·0-mm. (H.-L.) young of Calotes versicolor (Daud.) to show the relation of blood-vessels and nerves; *aci*, arteria carotis interna; *bpp*, basipterygoid process; *cp*, crista parotica; *cps*, cartilaginous connexion between stapes and the insertion plate of columella; *ct*, chorda tympani; *epl*, the extraplectral-parotic (processus) ligament; *fro*, foramen rotundum; *hf*, hypoglossal foramina; *hyn*, hypoglossal nerve; *ja*, Jacobson's anastomosis; *mus*. part of stylomastoid muscle spanning the extraplectral and crista parotica; *pd*, ligamentary processus dorsalis; *pi*, cartilaginous processus internus; *pie*, pars inferior of insertion plate; *pp*, processus paroticus; *pse*, pars superior of insertion plate; *q*, quadrate; *sa*, stapedial artery; *st*, stapes; *vcl*, vena capitis lateralis; *7g*, facial ganglion; *7h*, hyomandibular branch of facial nerve; *7p*, palatinus facialis; *IX*, glossopharyngeal nerve; *IXg*, ganglion on the IX; *X*, vagus nerve.

semicircular canal enters the cavum vestibulare posterius there is a short projection of cartilage (Text-fig. 15 c, *ise*) separating the inferior orifice of the posterior (*ipsc*) and the posterior opening of the lateral semicircular canals (*opl*).

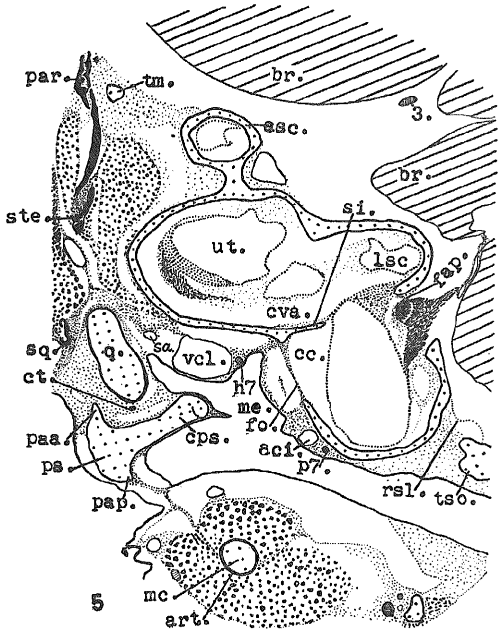
The foramen perilymphaticum noticed in the posterior wall of the cavum cochleare faces into the fissura metotica. Like Lacerta, the recessus scalae tympani of Calotes shows the same arrangement: the recessus scalae tympani medialis (covered over by connective tissue) and the recessus scalae tympani lateralis (covered over by secondary tympanic membrane) and the IX nerve pierce both to gain exit.

The Columella Auris.—In the fenestra vestibuli (Text-fig. 11; Text-fig. 13 A, *fo*) fits in the footplate or stapes (*st*) of the columella auris, a product of the visceral arch. The insertion plate (Text-fig. 11; Text-figs. 16 B, 16 C, *ip*) which fits into the tympanic membrane is connected with the stapes by a cartilaginous bar (the whole being called extracolumella) and shows the following projections: a long cartilaginous process directed anteroventrally—the pars inferior (Text-fig. 13 A; Text-fig. 4, *pie*) and the part of the plate which is posterodorsal to the connecting piece of cartilage (Text-figs. 11, 13 A, 16 B; Text-figs. 4, 5, *cps*)—the pars superior (Text-fig. 13 A; Text-fig. 4, *pse*). From the pars superior there are two short cartilaginous projections: one directed towards the quadrate—the processes accessorius anterior (Text-fig. 5, *paa*) from which a thin ligament arises and is inserted to the quadrate, and a posterior—the processus accessorius posterior (*pap*). From this posterior process, no connexion either cartilaginous or ligamentary is noticed with the ceratohyal, unlike what is described by Fuchs (1907), Kunkel (1912), and Shiino (1914) in various reptiles. In addition, starting from the pars inferior and passing over the pars superior there is a thick ligament (Text-fig. 4, *epl*) which meets the processus paroticus (*pp*) at the region where the processus dorsalis (*pd*) (see below) unites with the former. The chorda tympani (*ct*) passes dorsolaterally to this ligament. There is also a muscle (*mus*) arising from the insertion plate (from the pars superior region) and getting inserted to the crista parotica (*cp*) along with the stylohyoid muscle. Such a muscle is also noticed by Brock (1932) in Lygodactylus.

No reference is made by Gaupp (1900) to these ligamentary connexions. Rice (1920) described in Eumeces a parotic ligamentary connexion (with the chorda tympani passing laterally to this) and Fuchs described a connexion between the processus accessorius anterior and the quadrate. Versluys (1903) described a ligamentary connexion between insertion plate and parotic process in Pachydactylus; in Lygodactylus (Brock, 1932) a transient cartilaginous connexion with the parotic process with which the ceratohyal also united is noted. In Agama (Brock, 1932) and Varanus (Bahl, 1937) the parotic ligamentary connexion is described, and Versluys (1903) in his schematic figure of the columella auris for lizards shows a ligament arising from the pars inferior (as in Varanus, Bahl, 1937) and reaching the processus paroticus or intercalary. In Amphisbaena Versluys (1898) mentioned the absence of this connexion.

From the connecting cartilaginous rod between insertion plate and stapes arises the cartilaginous processus internus (Text-fig. 13 A; Text-fig. 4, *pi*) in Calotes and projects anteroventrally towards the quadrate with which it articulates as in Lacerta (Gaupp, 1900) and Agama (Brock, 1932). In Eumeces (Rice, 1920) it does not reach the quadrate. In Lygodactylus (Brock, 1932) and adult Chalcides (Haas, 1936) it is absent. According to Versluys (1898) the adult Scincidae lack it; in other lizards like Uroplates, Anguidae and embryos and adults of Geckonidae it is also absent (Versluys, 1903).

There is another ligamentary connexion in Calotes—the processus dorsalis (Text-figs. 11, 13 A, 16 B; Text-fig. 4, *pd*) uniting the connecting cartilaginous piece of the columella (*cps*) with the processus paroticus (*pp*). It arises dorsally from the columella at the region where the processus internus is given off ventrally. Versluys (1903) described, in this connexion, how the dorsal portion of the original cartilaginous processus dorsalis formed the intercalary or processus paroticus when it met the crista parotica, while the connexion between the intercalary and columella remained as a ligament.



TEXT-FIG. 5.

Transverse section of a 8·0-mm. (H.-L.) young of Calotes versicolor (Daud.) in the region of middle ear, ×55. *aci*, arteria carotis interna; *art*, articular; *asc*, anterior semicircular canal; *br*, brain; *cc*, cavum cochlearis; *cps*, connecting cartilage between stapes and insertion plate; *ct*, chorda tympani; *cva*, cavum vestibulare anterius; *fap*, foramen acusticum posterius; *fo*, foramen vestibuli; *h7*, hyomandibularis facialis; *lsc*, lateral semicircular canal; *mc*, Meckel's cartilage; *me*, middle ear; *paa*, processus accessorius anterior; *pap*, processus accessorius posterior; *par*, parietal; *ps*, pars superior of insertion plate; *p7*, palatinus facialis; *q*, quadrate; *rsl*, recessus scalae tympani lateralis; *sa*, stapedial artery; *si*, septum intervestibulare; *sq*, squamosal; *ste*, supratemporal; *tm*, taenia marginalis; *tso*, tuberculum spheno-occipitale; *ut*, utriculus; *vcl*, vena capitis lateralis; *3*, oculomotor nerve.

The processus dorsalis is absent in Eumeces (Rice, 1920), Lygodactylus (Brock, 1932), and adult Chalcides (Haas, 1936). In Varanus (Bahl, 1937) also a processus dorsalis is said to be absent; however, a ligamentary connexion in exactly the same position as the processus dorsalis is drawn (p. 159, Text-fig. 13); but the chorda tympani bears no relation to this. Having examined Varanus, I am inclined to consider the ligamentary connexion as a processus dorsalis, though the chorda tympani does not surround it from backwards.

The branches of the hyomandibular nerve (Text-fig. 4, *7h*, *7p*, *ct*), the jugular vein, and the stapedial artery (*sa*) bear typical relations with the processus dorsalis (*pd*), processus internus (*pi*), and the ligamentary pars superior-parotic connexion as described in Lacerta (de Beer, 1937).

4. The Orbitotemporal Region.

As in other lizards, the orbitotemporal region is characterized by the absence of a roof. The trabeculae (Text-fig. 12, *tr*) running anteriorly from the basal plate unite anteriorly to the hypophysial fenestra (*hyf*) forming the trabecula communis (*tc*). In Lacerta (Gaupp, 1900) and Eumeces (Rice, 1920) the trabecula communis runs anteriorly under the interorbital septum. In Calotes it stops short at the anterior end of the hypophysial fenestra. In Chelone Fuchs (1912) stated that the trabeculae did not enter into the formation of the interorbital septum.

The internal carotid artery becomes intracranial through the hypophysial fenestra.

The basipterygoid articulation is noticed as in Lacerta (Gaupp, 1900) and Eumeces (Rice, 1920) between the basitrabecular process of the trabecula (Text-fig. 11, *btp*) and the broad meniscus pterygoideus cartilage (*mp*), which represents the basal process of the pterygoquadrate. No connexion between the meniscus cartilage and the base of the processus ascendens (*pas*) is noticed in any of the stages of Calotes studied.

The interorbital septum (Text-fig. 11, *ios*) makes a sharp bend near the olfactory region. Near the olfactory capsule, the septum shows an anterior smaller (*f1*) and a posterior larger (*f2*) septal fenestra. Connecting the interorbital septum anteriorly and forming the anterior boundary of this large posterior fenestra there is the round bar of cartilage—the united preoptic pillar (*pop*) uniting posterodorsally with the planum supraseptale (*pls*). From the ventral aspect of the posterior portion of the planum supraseptale there descends a vertical pillar (*pios*) which meets the interorbital septum below and forms the posterior boundary of the large fenestra (*f2*).

In Lacerta (Gaupp, 1900), in the region corresponding to the preoptic pillar of Calotes, the anterior portion of the supraseptal cartilage is broad with a median depression; however, from the anterior portion of the planum there are two cartilaginous projections, one on each side, as in Calotes (Text-figs. 11, 12, *apls*). These two projections are just indicated in Eumeces (Rice, 1920). From the posterodorsal edge of the planum there arises in Lacerta the taenia marginalis, which, however, is wanting in Calotes. A small projection from the lateral portion of the planum represents, in Calotes, the anterior end of the taenia marginalis (*atm*); similarly a small projection from the anterior margin of the otic capsule represents the posterior reminiscence of this (*ptm*). In Lacerta (Gaupp, 1900) the taenia medialis arising from the posteroventral edge of the planum supraseptale meets and fuses with the vertical pila antotica; it is also connected with two more pillars —the pila accessoria (connecting with taenia marginalis) and pila metoptica (uniting and forming the subiculum infindibuli and cartilago hypochiasmatica). In Calotes since there is no taenia marginalis, there is no pila accessoria; the taeniae mediales (*tme*) progress towards the hypophysial fenestra and fuse. Slightly anteriorly to this fusion the taeniae are met by a short round obliquely vertical pillar (*chsp*) from the interorbital septum—the united cartilago hypochiasmatica, subiculum infundibuli, and pila metoptica. In Lacerta (de Beer, 1937) that part of the taenia in front of the pila accessoria is called taenia medialis, while that behind it is the metoptic pila. In Calotes, such a differentiation is not possible. The taenia posterior to this median cartilaginous pillar represents the reminiscence of the connexion of the taenia with the pila antotica.

The various foramina in this region may now be recounted:

(i) the two septal fenestra (Text-fig. 11, *f1*, *f2*) anteriorly do not transmit anything.

(ii) the optic fenestra (*of*) is bounded anteriorly by the vertical pillar (*pios*) of the interorbital septum; below by the united cartilago hypochiasmatica, subiculum infundibuli, pilae metopticae and interorbital septum, and dorsally by the taenia medialis.

(iii) the metoptic fenestra (*fm*) is bounded anteriorly by the cartilago hypochiasmatica (plus subiculum infundibuli and pilae metopticae), above by the posterior part of the taenia medialis, below by the trabecula, and posteriorly there is no definite boundary. The third and fourth cranial nerves take exit in this fenestra.

(iv) the prootic fenestra (in front of incisura prootica, *ipr*) is no definite fenestra; it may be said that the pila antotica (*pa*) and processus ascendens (*pas*) bound it anteriorly, while below it is bounded by the basal plate and behind by the auditory capsule and prefacial commissure (*pfc*). Dorsally it is not limited in Calotes, while in Lacerta (Gaupp, 1900) the taenia marginalis roofs it. It must, however, be noted that the trigeminal ganglion is lodged in an extracranial space, the cavum epiptericum, which is slightly posterior to the processus ascendens in the incisura externally to the skull wall.

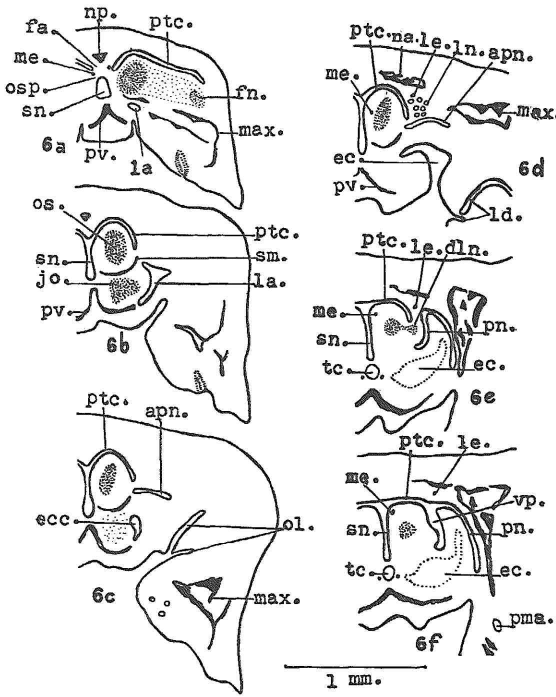
A sclerotic cartilage is well developed.

5. The Ethmoid Region.

Since the topography of the cartilages in the nasal region differs considerably from the descriptions of Lacerta (Gaupp, 1900) and Eumeces (Rice, 1920), I propose to describe in detail the olfactory region of Calotes.

The anterior sections of the nasal capsule in Calotes reveal that the fenestra narina (Text-fig. 14c, *an*) is lateral and this part of the olfactory sac, the cupola anterior (*ca*), is covered over by the anterior parietotectal cartilage. In Lacerta

(Gaupp, 1900) the median branch of the ethmoid nerve gets exit by the foramen apicalis situated one on each side in the cupola anterior; the fenestra superior is above and posterior to each apical foramen. In Calotes there is a gap between the nasal septum and the parietotectal cartilage (Text-fig. 14 A; Text-fig. 6 A, *fa*) and through this, the combined fenestrae apicales, the ramuli medialis (*me*) come out. A fenestra superior is absent in Calotes. Supporting Jacobson's organ, the lamina transversalis anterior (Text-figs. 14 B, 14 C, *la*) is noticed with its inner limb united (*clsn*) with the unfenestrated septum nasi (*sn*). A few sections posteriorly where Jacobson's organ is cut, it is seen as a discrete cartilage (Text-fig. 6 B, *la*); no projection of it enters into the floor of Jacobson's organ as in Ablepharus and Chalcides (Haas, 1935, 1936). In Calotes it divides into two, one partially embracing Jacobson's organ (Text-figs. 14 B, 14 C; Text-fig. 6 C, *ecc*) and the other (*apn*) situated dorsally to this but laterally to the parietotectal cartilage; this latter is an anterior extension of the paranasal cartilage. In Lacerta, the lamina transversalis anterior not only forms a support for Jacobson's organ but also a complete ring of cartilage (zona annularis) round it; in Calotes since the side wall is incomplete in this region there is no ring formation. Further from the posteromedian part of the lamina transversalis anterior there arises in Lacerta (Gaupp, 1900) the paraseptal cartilage (free from the nasal septum). It unites with the anterior portion of lamina orbitonasalis; in Calotes there is no paraseptal cartilage at all in this region. However, there is the process corresponding to the ectochoanal cartilage (*ecc*). The nasal glands appear (Text-fig. 6 D, *ln*) in the gap between the parietotectal (*ptc*) and the anterior portion of paranasal cartilage (*apn*); the ramus lateralis (*le*) of the ethmoid nerve is associated with these glands. This region would, therefore, correspond with the cavum conchale of Lacerta. The paranasal cartilage is unconnected with the parietotectal in this region nor does it form a concha nasalis by reduplication as in Lacerta and Eumeces. The lateral nasal glands are, therefore, not at all enclosed. In Text-fig. 6 E, the opening of the duct (*dln*) from these glands into the olfactory sac is noticed.



TEXT-FIGS. 6 A–6 F.

Consecutive transverse sections in the region of nasal capsule of 8·0-mm. (H.-L.) embryo of Calotes versicolor (Daud.). *apn*, anterior part of paranasal cartilage; *dln*, duct entering cavum nasale principale from lateral nasal glands; *ec*, recessus ectochoanalis; *ecc*, ectochoanal cartilage; *fa*, conjoint fenestrae apicalis; *fn*, fenestra narina; *jo*, Jacobson's organ; *la*, lamina transversalis anterior; *ld*, ductus nasolachrymalis; *le*, lateral ethmoid nerve; *ln*, lateral nasal glands; *max*, maxilla; *me*, median ethmoid nerve; *na*, nasal; *np*, nasal process of premaxilla; *ol*, opening of nasolachrymal ducts; *os*, cavum nasale principale; *osp*, orifice between septum nasale and parietotectal cartilage; *pma*, processus maxillaris anterior; *pn*, paranasal cartilage; *ptc*, parietotectal cartilage; *pv*, prevomer; *sm*, septomaxilla; *sn*, septum nasi; *tc*, trabecula communis; *vp*, vertical pillar.

However, in the 8·0 mm. young, the opening of this duct is slightly posterior to the vertical cartilage formed by the union of the paranasal and parietotectal cartilages. In this region (Text-fig. 6 E) the cavum extraconchale (*cc*) is also seen and this is embraced by the paranasal cartilage (*pn*) having assumed the shape of a horseshoe. The lateral ethmoid nerve (*le*), as in the previous figure, is external to the parietotectal cartilage (*ptc*). Posteriorly (Text-fig. 6 F) the parietotectal and paranasal cartilages unite forming a vertical pillar (*vp*) and still the ramus lateralis (*le*) is external to the cartilage. This pillar separating the olfactory from the extraconchal recess does not represent the fused posterior walls of the conchae nasales since the auditus concha in all the Lacertilia is posterior to the epiphaneal foramen; also it does not represent the crista semicircularis of mammals since that is also posterior to the epiphaneal foramen. The paranasal cartilage continues posteriorly into the lamina orbitonasalis (Text-figs. 14 A, 14 C, *lon*), the demarcating orifice being the epiphaneal between the two.

The epiphaneal foramen (Text-fig. 14 A, *fe*) is peculiarly disposed. The ramus lateralis nasi situated ventrally to the commissura spheno-ethmoidalis (*cse*) becomes intracranial when the latter unites with the lamina orbitonasalis (*lon*) and gets exit a few sections anteriorly. In Lacerta (Gaupp, 1900) and Eumeces (Rice, 1920) the ramus lateralis nasi gets out through the epiphaneal foramen and enters the cavum conchale by its anterior opening, the auditus concha.

The olfactory nerve running dorsomedially to the spheneth-moid commissure enters the fenestra olfactorium advehens by getting out through the foramen olfactoria evehens; this is exactly as in Lacerta (de Beer, 1937). The ethmoid nerve (ophthalmicus profundus V) enters the extracranial orbitonasal space (cavum orbitonasale) ventrally to the sphenethmoid commissure in Calotes and before entering the olfactory sac divides into two; the ramulus medialis enters by its own orifice in the cartilaginous wall and not by the advehent opening as in Lacerta and gets out through the conjoint apical orifice in Calotes. The passage of the lateral ramulus has been described above.

The width of the nasal capsule in the posterior region could only be ascribed to the formation of an extracranial portion since a concha nasalis is not formed in Calotes.

The hinder part of the nasal capsule is free from the nasal septum in Lacerta; it is also free ventrally in Calotes (Text-fig. 14 B) but attached to nasal septum dorsally by means of the lamina orbitonasalis. The free olfactory floor in the posterior region formed by the lamina orbitonasalis shows a projection by the side of the nasal septum. This projection represents the reminiscence of the paranasal connexion (*pps*).

The lamina orbitonasalis shows two projections at different levels. The anterior one at about the level of the vertical pillar referred to previously represents the processus maxillaris anterior (Text-figs. 14 B, 14 C; Text-fig. 6 F, *pma*). Arising from the posterior wall of the lamina orbitonasalis on either side of the interorbital septum (*ios*) there is a short projection which I have called the posterior laminal process (*plp*). This does not represent the posterior maxillary process, since in the 8·0-mm. stage this is noticed to arise from the posterior aspect of the lamina orbitonasalis and the posterior laminal process is also present.

6. The Pterygoquadrate.

The pterygoquadrate, it has already been pointed out, was noticed as dense mesenchyme in the 3·6-mm. stage extending anteriorly from the region where the future basitrabecular articulation would be formed. The next and subsequent stages show that an anterior pterygoid process is not developed and the processus maxillaris posterior of the lamina orbitonasalis represents the remnants of the ethmoid connexions of the pterygoquadrate. A processus ascendens is well formed (Text-fig. 11; Text-fig. 12, *pas*) and does not show any connexion dorsally with the otic capsule as in Platydactylus (Hafferl, 1921). In adult Varanus (Bahl, 1937) the dorsal part of the processus ascendens is united with the otic capsule. Narayanaswamy Iyer (1943) also described a dorsal cartilaginous otic-ascendens connexion in Calotes. There is a meniscus pterygoideus (Text-fig. 11, *mp*) cartilage between the ventral portion of the processus ascendens and the basitrabecular projection (*btp*), representing the basal process of the pterygoquadrate.

The otic articulation of the pterygoquadrate is noticed as in other lizards (Lacerta Gaupp, 1900; Eumeces Rice, 1920); the dorsal portion of the quadrate part of the pterygoquadrate (Text-fig. 11, *oa*) articulates with the crista parotica (*cp*) and the processus paroticus (*pp*).

When the quadrate becomes ossified, the anterior crescentic portion of it forms an 'auditory cup' for the attachment of the anterior margin of the tympanic membrane.

The two rami of Meckel's cartilage (Text-fig. 7, *mc*) are almost straight circular rods united at the tip (*sm*), while posterior to the region of articulation with the quadrate (*aq*) is the processus retroarticularis (*pra*). It is interesting to note that, as in other lizards, Meckel's cartilage chondrifies much earlier than the neurocranium.

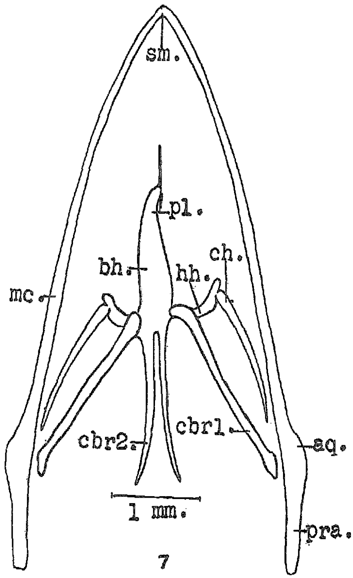
7. The Hyoid Apparatus.

The dorsal part of the hyoid arch, viz. the columella auris, was described in connexion with the otic capsule. The basihyal (Text-fig. 7, *bh*) gives rise anteriorly to a processus lingualis or entoglossus (*pl*), which enters the tongue, and to two lateral processes, one from each side, the hypohyal (*hh*). From each hypohyal (*hh*) extends the ceratohyal (*ch*) of its side. As already said, there is no connexion between the processus accessorius posterior of the columella auris and the ceratohyal.

From the basihyal there project posteriorly, the first (*cbr1*) and second (*cbr2*) ceratobranchials; ceratobranchial 1 is articulated with the basihyal by a ball and socket arrangement (Gnanamuthu, 1937; Narayanaswamy Iyer, 1943). Unlike Lacerta (Gaupp, 1900) and Eumeces (Rice, 1920) the ceratobranchial 2 is a complete rod of cartilage and not observed to be in two parts.

II. Osteocranium of a just-hatched young of Calotes versicolor (Daud.), H.-L. 8·0 mm.

I am describing the cranial bones in a just-hatched young of Calotes with a head-length of 8·0 mm. As already



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TEXT-FIG. 7.

Meckel's cartilage and hyobranchial apparatus of a 8·0-mm. (H.-L.) embryo of Calotes versicolor (Daud.). *aq*, articular facet for quadrate; *bh*, basihyal; *cbr1*, ceratobranchial 1; *cbr2*, ceratobranchial 2; *ch*, ceratohyal; *hh*, hypohyal; *mc*, Meckel's cartilage; *pl*, processus lingualis; *pra*, processus retroarticularis; *sm*, symphysis meckelii.

said, the adult skull has been described by Narayanaswamy Iyer (1943).

Membrane bones.

The nasal (Text-fig. 16 A, *na*) starts on each side of the nasal process of the premaxilla (*pmx*) posterior to the conjoint apical foramen. It is disposed on the parietotectal cartilage and extends as far as the epiphaneal foramen. In the adult, also, it is paired (Narayanaswamy Iyer, 1943). It is unpaired in Varanus (Bahl, 1937).

The frontal (*fr*) arises over the lamina orbitonasalis posterior to the epiphaneal foramen, medially to the prefrontals (*prf*) and dorsolaterally to the sphenethmoid commissure. The two bones are disposed near each other on the preoptic pillar (Text-fig. 16 C, *pop*), lateral to the supraseptal (*ps*), and end postoptically diverging from each other. In the adult (Narayanaswamy Iyer, 1943) the two frontals unite to form a single bone and the gap between the two bones in this stage is bridged by osseous tissue.

Each parietal (Text-figs. 16 A, 16 C, *par*) arises medially at the posterior end of the diverging frontal and the cranial roof between the two parietals is bridged by connective tissue; in the region of the anterior semicircular canal, the reminiscent taenia marginalis projection from the otic capsule is dorsal and widely separated from the parietal and the bone ends on the crista parotica (*cp*). In Lacerta (de Beer, 1937) the frontals and parietals are associated with the taenia marginalis, but in Calotes, as already noted, this cartilage is not formed. In the adult Calotes (Narayanaswamy Iyer, 1943) the two parietals unite to form a large bone with a median orifice—the pineal orifice. From the parietal there are two posterior paroccipital processes, each coming in contact with the exoccipital and quadrate of its side.

The septomaxilla arises dorsally to the union of the lamina transversalis anterior with the nasal septum and lies dorsally to this cartilage and Jacobson's organ (see Text-fig. 6 B, *sm*). It forms the floor of the olfactory sac (Text-fig. 16 B, *smx*) and disappears where the cavum extraconchale enters the choana. In the adult (Narayanaswamy Iyer, 1943) the septomaxilla is disposed ventrally to the nasal process of the premaxilla and medially to the maxilla, in the olfactory region. In Chameleon (Haas, 1937) the septomaxilla is wanting.

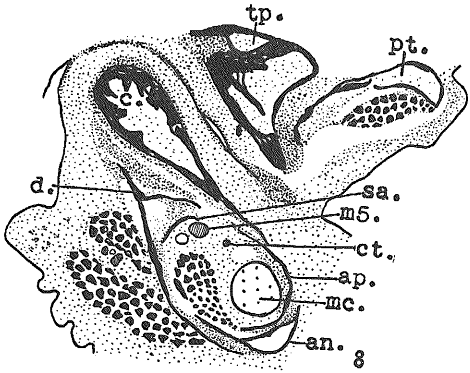
The prefrontal (Text-figs. 16 A, 16 C, *prf*) arises on the postero-lateral surface of the nasal capsule, and in the region of the lateral nasal glands they form a lateral boundary for them.

In the region of the lamina orbitonasalis and the sphenethmoid commissures, each prefrontal shows two limbs, a flat and transverse one externally to the frontal and a flat and vertical depending downwards (towards the palatine) and investing the posterolateral face of lamina orbitonasalis. This vertical limb of the prefrontal lies medially to the nasolachrymal opening (Text-fig. 16 C, *pnl*). Between the two vertical limbs of the prefrontals is noticed the orifice which is separated into right and left by the anterior end of the interorbital septum; the two sphenethmoid commissures arise from the dorsal end of this septum and proceed towards the lamina orbitonasalis. The orifice by the side of the nasal septum through which the ethmoid nerve enters the olfactory capsule is the posterior part of the cavum orbitonasale. In the young as well as in the adult (Narayanaswamy Iyer, 1943), since a lachrymal bone is absent, the prefrontal touches the maxilla on the side, and the latter bone, therefore, forms the external boundary of the nasolachrymal orifice.

The prevomer (Text-fig. 16 B, *pv*) appears as a single ossification below the nasal septum and also below the lamina orbitonasalis. Posteriorly where the trabecula communis appears as a separated piece of round cartilage below the nasal septum, the anterior part of palatine appears on each side dorsally to the now separate prevomers and a few sections posteriorly the prevomers disappear.

The palatine (Text-figs. 16 A, 16 B, 16 C, *pal*) arises behind the prevomers and while forming the median boundary of the choana, also gives rise to a maxillary process behind the lamina orbitonasalis. In this region the sections reveal, below the palatine and externally to the palatine and maxilla, two round cartilages; both these are posterior projections from the lamina orbitonasalis running parallel, and the lower one of them represents the processus maxillaris posterior. Similar isolated nodules of cartilage situated one above the other have also been noticed dorsally to the palatine in the processus maxillaris posterior region of L a c e r t a (Gaupp, 1900). The inner border of the palatine in C a l o t e s is noticed ventrally to a region where the lamina orbitonasalis gives rise posteriorly to a blunt cartilaginous process.

Extending from the posterior margin of the palatines are the two pterygoids (Text-figs. 16 A, 16 B, 16 C, *pt*). Each pterygoid is flat anteriorly as the palatine and has a ridge ventromedially, and in the region of the ectopterygoid (transpalatine) (Text-fig. 16 B, *ecp*) shows an enlargement. Posterior to the basipterygoid articulation (*bpp*) it becomes dorsoventrally flattened, and



TEXT-FIG. 8.

Transverse section of 8·0-mm. (H.-L.) young of Calotes versicolor (Daud.) in the region of the ectopterygoid-pterygoid-coronoid articulation. ×55. *an*, angular; *ap*, articular (with prearticular); *c*, coronoid; *ct*, chorda tympani; *d*, dentary; *mc*, Meckel's cartilage; *m5*, ramus mandibularis V; *pt*, pterygoid; *sa*, supra-angular; *tp*, ectopterygoid (transpalatine).

it ends articulating with the ventral end of the quadrate (*q*). Between the palatine, pterygoid, maxilla, and ectopterygoid is the mediopalatinal fossa (*mpf*).

The ectopterygoid (transpalatine) (Text-figs. 16 A, 16 B, *ecp*) spans the jugal-maxilla and the lateral limb of the pterygoid. At the region of articulation with the pterygoid, the coronoid process of the lower jaw (Text-fig. 8, *c*) also enters and the three bones articulate with thick connective tissue in between them.

The premaxilla (Text-figs. 16 A, 16 B, 16 C, *pmx*) is formed by the fusion of the two premaxillae; dorsally there is a large nasal process, which lies over the nasal septum and extends mesially to the two nasals about half the length of the latter. It carries three teeth and also an anteriorly directed dentinal egg tooth (*et*). Ventrally there is a short median prevomerine projection (Text-fig. 16 B).

On each side of the premaxilla the maxilla (Text-figs. 16 A, 16 B, 16 C, *mx*) forms the outer ventral boundary of the orbit along with the jugal; the anterior boundary of the orbit is formed by the facial process of the maxilla and the prefrontal. The maxilla also sends a process upwards between the prefrontal and nasal. This is the nasal process of the maxilla.

The dentition of the maxilla and premaxilla in the adult Calotes is described by Narayanaswamy Iyer (1943).

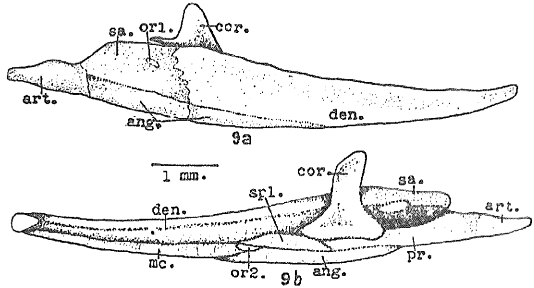
The fenestra narina (Text-figs. 16 A, 16 C, *an*) is lateral and is situated dorsally on the maxilla, but slightly posterior to where the latter meets the premaxilla.

The jugals are broad bones (Text-figs. 16 A, 16 C, *ju*); the anterior extension of each jugal is met with in the anterior orbital region, in association with the maxilla and in the region of the ectopterygoid; the latter articulates with the jugal and maxilla. Posterior to the maxilla, it broadens vertically forming the posterior border of the orbit along with the postfrontal; forming the supratemporal arcade, it ends dorsally to the quadrate where it is separated from the posterior process of the parietal by the squamosal and supratemporal.

The squamosal (Text-figs. 16 A, 16 B, 16 C, *sq*) forms the posterior portion of the supratemporal arcade and ends on the crista parotica (*cp*) externally to the supratemporal.

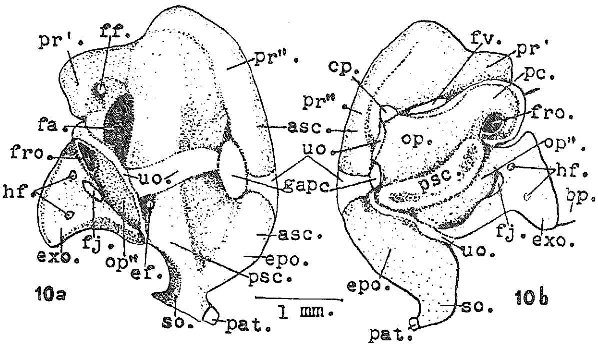
The supratemporal (tabular, Narayanaswamy Iyer, 1943) (Text-figs. 16 A, 16 C, *ste*) arises over the crista parotica internally to the squamosal and runs on the ventrolateral aspect of the posterior process of the parietal. The bone in the adult is not associated with the prootic as in Varanus (Bahl, 1937).

The postfrontal (Text-figs. 16 A, 16 B, 16 C, *pfr*) forms along with the lateral supraorbital extension of the frontal and parietal the posterior boundary of the orbit. Each postfrontal has three projections, one dorsal meeting the fronto-parietal



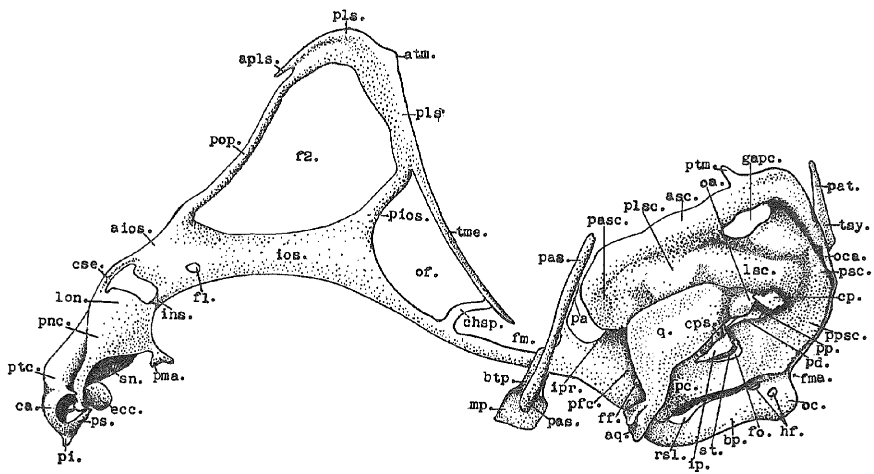
TEXT-FIGS. 9 A, 9 B.

The lower jaw of a 8·0-mm. (H.-L.) young of Calotes versicolor (Daud.), 9 A, outer aspect; 9 B, median aspect. *ang*, angular; *art*, articular (with prearticular); *cor*, coronoid; *den*, dentary; *mc*, Meckel's cartilage; *or1*, orifice for the lateral cutaneous branch of mandibular V; *or2*, orifice for the main trunk of alveolaris inferior nerve; *pr*, prearticular part of articular; *sa*, supra-angular; *spl*, splenial.



TEXT-FIGS. 10 A, 10 B.

Otic capsule of a 8·0-mm. (H.-L.) young of Calotes versicolor (Daud.), (alizarin preparation); 10 A, inner view; 10 B, outer view. *asc*, anterior semicircular canal; *bp*, basal plate; *cp*, crista parotica; *ef*, foramen endolymphaticus; *epo*, epiotic; *exo*, exoccipital; *fa*, foramen acusticum; *ff*, facial foramen; *fj*, foramen jugulare; *fro*, foramen rotundum; *fv*, fenestra vestibuli; *gapc*, gap between the anterior and the other semicircular canals; *hf*, hypoglossal foramina; *op*, opisthotic in the lateral semicircular canal region; *op″*, opisthotic in the posterior semicircular canal region; *pat*, processus anterior tecti; *pc*, prominentia cochlearis; *pr′*, prootic outside the otic capsule; *pr″*, prootic in the anterior semicircular canal region; *psc*, posterior semicircular canal; *so*, supra-occipital; *uo*, unossified parts.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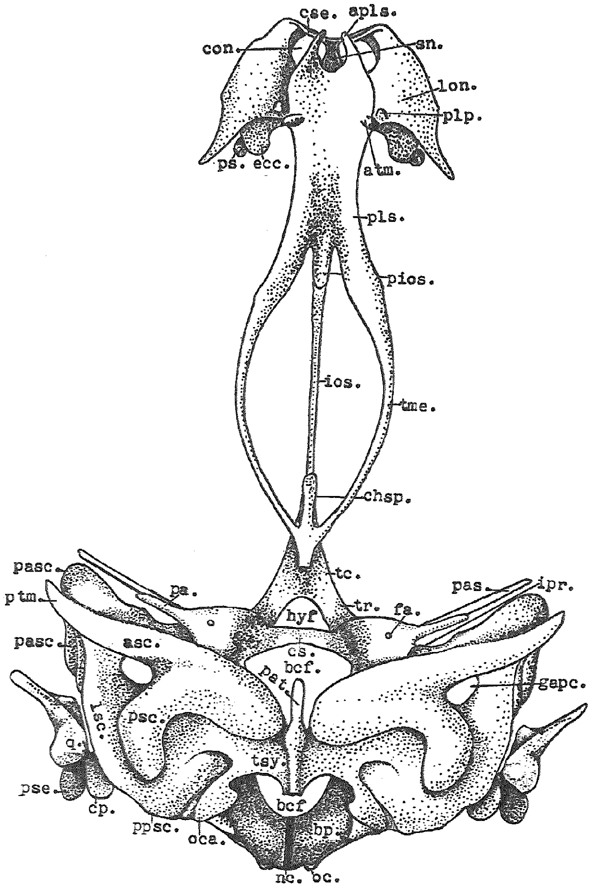
TEXT-FIG. 11.

Text-fig. 11.

The chondrocranium of a 8·0-mm. (H.-L.) embryo of Calotes versicolor (Daud.), side view of model, ×35; Meckel's cartilage and the right otic capsule are not included. *aios*, anterior portion of interorbital septum; *apls*, anterior projection from the planum supraseptale; *aq*, articular facet for quadrate; *asc*, anterior semicircular canal; *atm*, anterior projection of taenia marginalis; *bp*, basal plate; *btp*, basitrabecular process; *ca*, cupola anterior; *chsp*, united cartilago hypochiasmatica, subiculum infundibuli and pilae metopticae; *cp*, crista parotica; *cps*, cartilage connecting stapes with insertion plate; *cse*, commissura sphenoethmoidalis; *ecc*, ectochoanal cartilage; *f1*, anterior fenestra in interorbital septum; *f2*, larger fenestra in the same; *ff*, facial foramen; *fm*, fenestra metoptica; *fma*, foramen magnum; *fo*, fenestra vestibuli; *gapc*, gap between the anterior and other semicircular canals; *hf*, hypoglossal foramina; *ins*, region where the interorbital septum continues into the nasal septum; *ios*, interorbital septum; *ip*, insertion plate of extra-columella; *ipr*, incisura prootica; *lon*, lamina orbitonasalis *lsc*, lateral semicircular canal; *mp*, meniscus pterygoideus *oa*, otic articulation of quadrate; *oc*, occipital condyle *oca*, occipital arch; *of*, optic fenestra; *pa*, pila antotica *pas*, processus ascendens; *pasc*, prominentia ampullari of the anterior semicircular canal; *pat*, processus anterio tecti; *pc*, prominentia cochlearis; *pd*, processus dorsalis *pfc*, prefacial commissure; *pi*, processus alaris inferior *pios*, cartilaginous pillar uniting interorbital septum wit planum supraseptale; *pls*, planum supraseptale; *plsc* prominentia ampullaris of the lateral semicircular canal *pma*, processus maxillaris anterior; *pnc*, paranasal carti lage; *pop*, preoptic pillar; *pp*, processus paroticus; *ppsc* prominentia ampullaris of the posterior semicircula canal; *ps*, processus alaris superior; *psc*, posterior semi circular canal; *ptc*, parietotectal cartilage; *ptm*, posterio part of taenia marginalis; *q*, quadrate; *rsl*, recessus scala tympani lateralis; *sn*, septum nasi; *st*, stapes; *tme*, taeni medialis; *tsy*, tectum synoticum.



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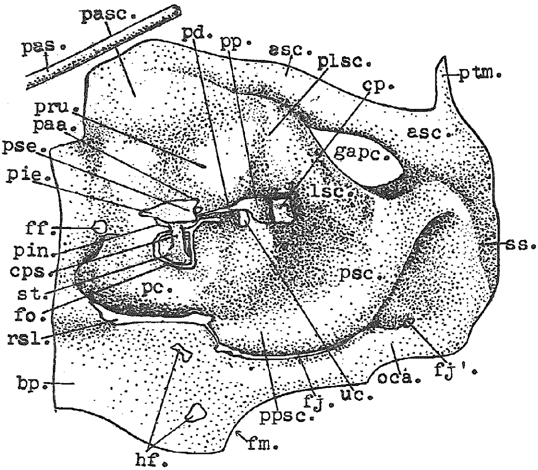
TEXT-FIG. 12.

suture, another ventral articulating with the jugal, while a posterior third not only articulates with the upper margin of the jugal but also with the squamosal; the squamosal articulation is noticed only in the adult condition and not in the young (Text-fig. 16 c). Thus the superior temporal arch is completed anteriorly by this bone.

Though in Agamids a postfrontal is described as absent (Brock, 1932) when the superior temporal arch is formed by the postorbital, I call the bone in the Agamid Calotes, a postfrontal. According to Brock, the single bone found in this region of Pachydactylus and Mabuia is apposed to the frontal and parietal (a criterion according to Camp (1923) of the postfrontal), while in Agama it is apposed to the parietal only, and is therefore called the postorbital. Following Camp, 'the postorbital lies between postfrontal, parietal, squamosal and jugal in position ventral and posterior to postfrontal'. Since in Calotes the bone abuts against the suture between frontal and parietal, I have called it postfrontal.

TEXT-FIG. 12.

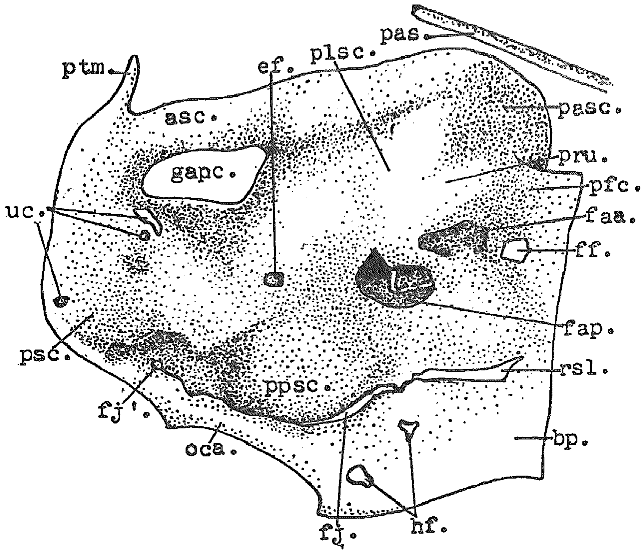
The chondrocranium of a 8·0-mm. (H.-L.) embryo of Calotes versicolor (Daud.), dorsal view, ×35; the model is so arranged that the planum supraseptale is at right-angles to the otic capsules. *apls*, anterior projection from the planum supraseptale; *asc*, anterior semicircular canal; *atm*, anterior projection of taenia marginalis; *bcf*, basicranial fenestra; *bp*, basal plate; *chsp*, united cartilago hypochiasmatica, subiculum infundibuli and pilae metopticae; *con*, cavum orbitonasale; *cp*, crista parotica; *cs*, crista sellaris; *cse*, commissura sphenoethmoidalis; *ecc*, ectochoanal cartilage; *fa*, foramen abducens; *gapc*, gap between anterior and the other semicircular canals; *hyf*, hypophysial fenestra; *ios*, interorbital septum; *ipr*, incisura prootica; *lon*, lamina orbitonasalis; *lsc*, lateral semicircular canal; *nc*, notochord; *oc*, occipital condyle; *oca*, occipital arch; *pa*, pila antotica; *pas*, processus ascendens; *pasc*, prominentia ampullaris of the anterior semicircular canal; *pat*, processus anterior tecti; *pios*, pillar between the interorbital septum and planum supraseptale; *plp*, posterior laminal process; *pls*, planum supraseptale; *ppsc*, prominentia ampullaris of the posterior semicircular canal; *ps*, processus alaris superior; *psc*, posterior semicircular canal; *pse*, pars superior of extraplectral; *ptm*, posterior part of taenia marginalis; *q*, quadrate; *sn*, septum nasi; *tc*, trabecula communis; *tme*, taenia medialis; *tr*, trabecula; *tsy*, tectum synoticum.



TEXT-FIG. 13 A.

TEXT-FIGS. 13 A AND 13 B.

The otic capsule with adjacent basal plate of a 8·0-mm. (H.-L.) embryo of Calotes versicolor (Daud.), ×50. 13 A, outer view, 13 B, median view of model. *acs*, anterior semicircular canal; *bp*, basal plate; *cp*, crista parotica; *cps*, connecting cartilage between stapes and insertion plate of extracolumella; *ef*, foramen endolymphaticus; *faa*, foramen acusticus anterius; *fap*, foramen acusticus posterius; *ff*, facial foramen; *fj*, foramen jugulare; *fj'*, posterior part of jugular foramen; *fm*, foramen magnum; *fo*, foramen vestibuli; *gapc*, gap between the anterior and the other semicircular canals; *hf*, hypoglossal foramina; *lsc*, lateral semicircular canal; *oca*, occipital arch; *paa*, processus accessorius anterior; *pas*, processus ascendens; *pasc*, prominentia ampullaris of the anterior semicircular canal; *pc*, prominentia cochlearis; *pd*, processus dorsalis; *pfc*, prefacial commissure; *pie*, pars inferior of extraplectral; *pin*, processus internus; *plsc*, prominentia ampullaris of the lateral semicircular canal; *pp*, processus paroticus; *ppsc*, prominentia ampullaris of the posterior semicircular canal; *pru*, prominentia recessus utriculus; *psc*, posterior semicircular canal; *pse*, pars superior of the extra-



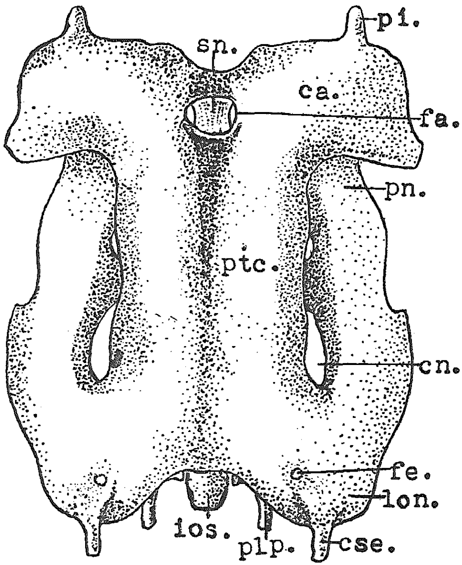
TEXT-FIG. 13 B.

plectral; *ptm*, posterior part of taenia marginalis; *rsl*, recessus scalae tympani lateralis; *ss*, sinus superior; *st*, stapes; *uc*, unchondrified areas in the otic capsule.

TEXT-FIGS. 14 A–14 C (pp. 274–6).

The olfactory capsule of 8·0-mm. (H.-L.) embryo of Calotes versicolor (Daud.), ×50. 14 A, dorsal view; 14 B, ventral view; 14 C, lateral view. *an*, anterior naris; *apn*, anterior part of paranasal cartilage; *ca*, cupola anterior; *clsn*, union of lamina transversalis anterior and septum nasi; *cn*, cavum conchale; *cse*, commissura sphenoethmoidalis; *ecc*, ectochoanal cartilage; *fa*, united foramina apicalis; *fe*, foramen epiphaniale; *ios*, interorbital septum; *la*, lamina transversalis anterior; *lon*, lamina orbitonasalis; *pi*, processus alaris inferior; *plp*, posterior laminal process; *pma*, processus maxillaris anterior; *pn*, paranasal cartilage; *pps*, posterior part of paraseptal cartilage; *ps*, processus alaris superior; *ptc*, parietotectal cartilage; *sn*, septum nasi; *vp*, vertical process.

The parasphenoid underlies the ventral surface of the hypophysial fenestra, leaving anteriorly a small foramen (Text-figs. 16 A, 16 B, *fo*), and runs anteriorly under the interorbital



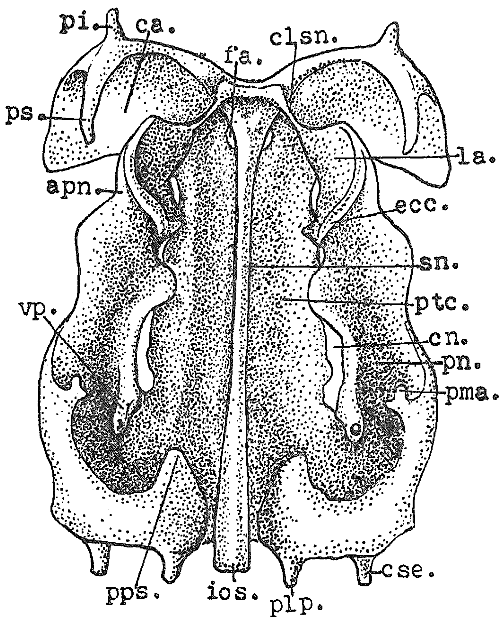
TEXT-FIG. 14 A (see p. 273).

septum (*r*). The median part under the hypophysial fenestra also extends under the basipterygoid processes (*bpp*), while dorsally it is united with the basisphenoid (*bs*). In Lacerta (de Beer, 1937) the parasphenoid arises in two lateral and a median centre which unite later. In the adult this bone undergoes fusion with the overlying basisphenoid and the composite bone is called 'sphenoid'.

In each eye-ball of Calotes there are twelve sclerotic bones.

A quadratojugal, postorbital, and supraorbitals are absent; also no osteoscutes are seen in Calotes.

The prearticular (Text-fig. 9 B, *pr*) arises on the inner aspect of Meckel's cartilage and fuses with the cartilaginous articular (*art*); the chorda tympani which enters posteriorly to the quadrato-meckelian articulation runs between Meckel's cartilage and articular.



TEXT-FIG. 14 B (see p. 273).

The supra-angular (Text-figs. 9 A, 9 B, *sa*) is noticed on the external surface of Meckel's cartilage above the angular; the posterior portion of the dentary covers a portion of the supra-angular as seen in sections (see Text-fig. 8, *d*).

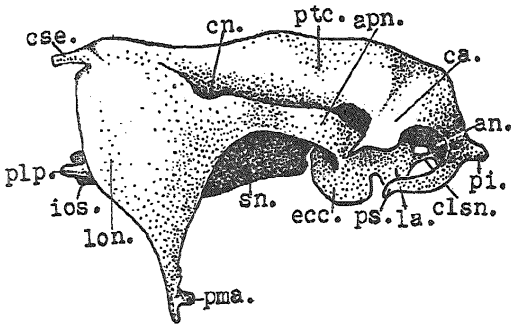
The angular (Text-figs. 9 A, 9 B, *ang*) arises on the ventro-median part of Meckel's cartilage and covers the internal portion of the prearticular, and the upper portion of the angular is also covered over by the dentary (*den*).

The splenial (Text-fig. 9 B, *spl*) arises on the middle portion of Meckel's cartilage medially and is anterior to the angular.

The coronoid (Text-figs. 9 A, 9 B, *cor*) arises dorsomedially to the splenial and forms the anterior limit of the supra-angular.

Orifices in the Lower Jaw.

1. The orifice in the dorsal aspect of the retro-articular



TEXT-FIG. 14 C (see p. 273).

process posterior to the quadrate articulation for the entry of the chorda tympani is mentioned above.

2. Between the supra-angular and articular portion, medially in front of the quadrate articulation, the ramus mandibularis V enters the lower jaw.

3. Just posterior to the dentary, in a notch in this bone laterally, there is an orifice in the supra-angular for a lateral cutaneous branch of mandibular V (Text-fig. 9 A, *or1*).

4. Anterior to the splenial there is an orifice for the passage of the main trunk of the alveolaris inferior (Text-fig. 9 B, *or2*).

5. A number of small orifices in the lateral aspect of the dentary for smaller branches of the alveolaris inferior are noticed.

The Cartilage Bones.

The basioccipital (Text-fig. 16 B, *bo*) appears as dorsal and ventral lamellae in the posterior region of the basal plate; the ventral lamella extends and there is a gap between it and the parasphenoid (Text-fig. 16 B, *pas*) anteriorly. The notochord is still seen to be wedged in the basal plate. The cartilaginous process (tuberculum spheno-occipitale) arising from the ventral aspect of the basal plate (Text-fig. 5, *tso*) is not yet invaded by bone.

In the adult (Narayanaswamy Iyer, 1943) the basioccipital is separated from the anterior 'sphenoid'.

The ossifications in the otic capsule and the tectum are clearly seen. The demarcations between the anterior prootic, dorsal supraoccipital (plus epiotic) and posterior exoccipital (plus opisthotic) are wide unossified areas in the capsule. However, in the adult these separating areas disappear.

The supraoccipital (Text-figs. 10 A, 10 B, *so*) arises perichondrally on the upper and lower aspects of the tectum connecting the posterior portion of the otic capsules. The anterior part of the processus anterior tecti (*pat*) is left unossified and between the parietals and the supraoccipital, on each side of the process, there is a gap where the cranial cavity is covered over by connective tissue. The epiotic (*epo*), with which the supraoccipital is continuous, is noticed in the sinus superior region (the posterior part of the anterior semicircular canal (Text-fig. 10 A, *asc*) and the superior part of the posterior semicircular canal (*psc*)) and extends medially as far as the inferior opening of the posterior semicircular canal, enclosing the endolymphatic foramen (*ef*).

The exoccipitals (Text-figs. 10 A, 10 B, *exo*) ossify perichondrally in the two occipital arches and each exoccipital unites with the opisthotic of its side to form a composite bone—the oto-occipital. The extension of each opisthotic is as follows: posterior face of cochlear portion (Text-fig. 10 B, *op*), behind fenestra vestibuli and below the crista parotica and in the posterior part of lateral (Text-fig. 16 A, *op'*) and inferior portion of posterior semicircular canal (Text-fig. 16 A; Text-figs. 10 A, 10 B, *op''*). Dorsally to the anterior hypoglossal foramen the opisthotic (Text-fig. 16 B, *ope*, *exo*; Text-fig. 10 B, *op*, *op''*, *exo*)

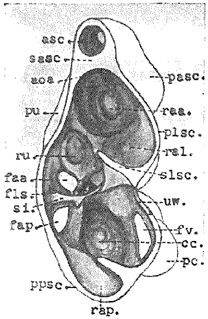


FIG. 15 A.

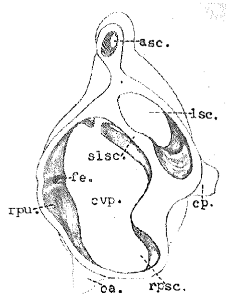


FIG. 15 B.

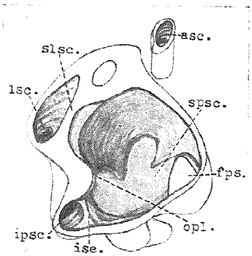


FIG. 15 C.

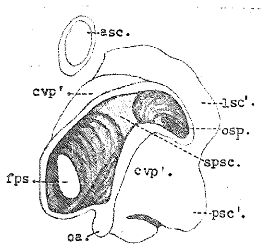


FIG. 15 D.

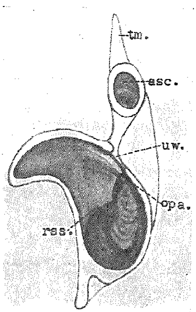


FIG. 15 E.

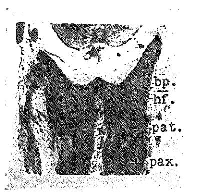


FIG. 15 F.

TEXT-FIGS. 15 A-15 F.

unites with the exoccipital. The foramen rotundum (Text-fig. 16 B, *fro*) is bounded, when viewed in the ventral aspect of the skull, anteriorly by opisthotic, posteriorly by exoccipital (*exo*), laterally by both these, and medially there is the cartilaginous basal plate. The opisthotic (Text-fig. 10 A, *op″*) when viewed on the medial aspect of the skull, forms the posterior boundary of the foramen rotundum (*fro*) and making an arch reaches the dorsal part of the exoccipital (*exo*).

TEXT-FIGS. 15 A–15 F.

15 A. Anterior part of the otic capsule of 8·0-mm. (H.-L.) embryo of Calotes versicolor (Daud.), model viewed from the posterior aspect, ×50. 15 B. Slightly posterior to fig. 15 A, viewed from the posterior aspect, ×50. 15 C. Posterior to fig. 15 B, viewed from the anterior aspect, ×50. 15 D. Same as fig. 15 C, viewed from the posterior aspect (only the outline position of the anterior semicircular canal is shown), ×50. 15 E. Anterior aspect of the posterior part of the otic capsule, ×50. 15 F. The occipito-atlantic region of a 3·6-mm. (H.-L.) embryo of Calotes versicolor (Daud.), ×70. *aoa*, anterior opening of the anterior semicircular canal; *asc*, anterior semicircular canal; *bp*, basal plate; *cc*, cavum cochlearis; *cp*, crista parotica; *cvp*, cavum vestibulare posterior; *cvp′*, external aspect of cavum vestibulare posterior; *hf*, hypoglossal foramen; *faa*, foramen acusticum anterius; *fap*, foramen acusticum posterius; *fe*, foramen endolymphaticus; *fls*, lateral foramen in the intervestibular septum; *fps*, foramen pro sinu; *fv*, fenestra vestibuli; *ipsc*, inferior opening of the posterior semicircular canal; *ise*, incomplete septum; *lsc*, lateral semicircular canal; *lsc′*, external aspect of lateral semicircular canal; *oa*, occipital arch; *opa*, posterior orifice of the anterior semicircular canal; *opl*, posterior orifice of the lateral semicircular canal; *osp*, superior orifice of the posterior semicircular canal; *pasc*, prominentia ampullaris of the anterior semicircular canal; *pat*, pleurocentrum of atlas vertebra; *pax*, pleurocentrum of axis vertebra; *pc*, prominentia cochlearis; *plsc*, prominentia ampullaris of the lateral semicircular canal; *ppsc*, prominentia ampullaris of the posterior semicircular canal; *psc′*, external aspect of the posterior semicircular canal; *pu*, prominentia utricularis; *raa*, recessus ampullaris of the anterior semicircular canal; *ral*, recessus ampullaris of the lateral semicircular canal; *rap*, recessus ampullaris of the posterior semicircular canal; *rpsc*, recessus of the posterior semicircular canal; *rpu*, recessus of the utriculus; *rss*, recessus sinus superior; *ru*, recessus utriculus (in the cavum vestibulare anterior); *sasc*, septum of the anterior semicircular canal; *si*, septum intervestibulare; *slsc*, septum of the lateral semicircular canal; *spsc*, septum of the posterior semicircular canal; *tm*, posterior part of taenia marginalis; *uw*, unchondrified wall in the otic capsule.

The opisthotic is demarcated from the anterior prootic by an unossified part of the lateral semicircular canal above the fenestra vestibuli and in front of crista parotica.

Between the arch of the opisthotic (Text-fig. 10 A, *op″*), the epiotic above and the prootic anteriorly, there is an unossified area (*uo*) in the otic capsule. The prootic is an ossification in the anterior part of the otic capsule. The extension of the prootic is as follows: anterior semicircular canal as far as the middle of the gap (*gapc*) between it and otic capsule (Text-fig. 10 A, *pr″*); lateral ampullary region, anterior border of fenestra vestibuli enclosing the facial foramen (*ff*) and extending towards the basipterygoid process in the basal plate; medially it forms the posterior boundary of the foramen acusticum posterius (*fa*) (but separated from the opisthotic by an unossified portion (*uo*)).

In Lygosoma (Pearson, 1921) the prootic is described as extending as far as the crista parotica.

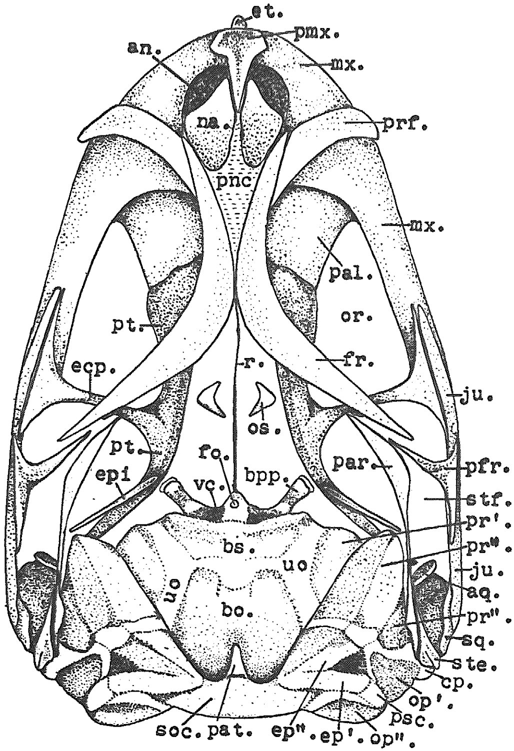
The basisphenoid in Calotes (Text-fig. 16 A, *bs*) appears in the crista sellaris, basitrabecular processes, and in the trabeculae near the crista; the ossification, as already noted (cf. parasphenoid), is dorsal to the parasphenoid and between this membrane bone and the basisphenoid laterally there is the parabasal or Vidian canal (Text-fig. 16 A, *vc*) through which the palatinus facialis nerve and the internal carotid artery pass. In the adult the basisphenoid fuses with the parasphenoid to form a 'sphenoid', as already described.

In Lacerta (de Beer, 1937) the presphenoid, basisphenoid, exoccipitals, supra-occipital, the epi-, pro-, and opisthotics and parasphenoid fuse to form a composite bone—the os basilare commune. In Calotes the basisphenoid, parasphenoid, ex- and supra-occipitals, epi-, pro-, and opisthotics and pleurosphenoids fuse to form a composite structure.

In Calotes the two orbitosphenoids (Text-fig. 16 A, *os*) are ossifications in the dorsal aspect of the taenia medialis.

A presphenoid is described in Lacerta (Gaupp, 1906) as an ossification in the posterior part of trabecula communis. I am not able to see this in sections of 8·0-mm. young of Calotes studied.

The pleurosphenoid ossifies in the pila antotica.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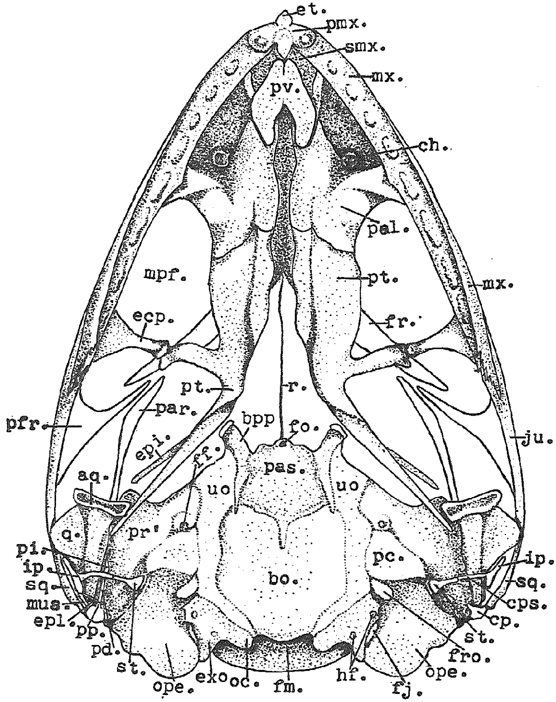
TEXT-FIG. 16 A.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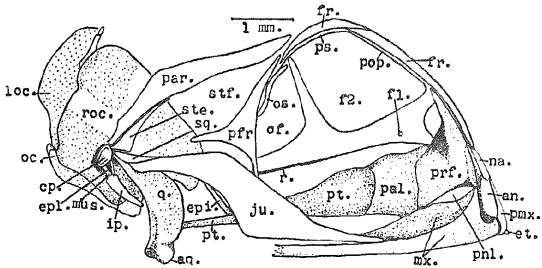
TEXT-FIG. 16 B.



TEXT-FIG. 16 C.

TEXT-FIGS. 16 A–16 C.

Osteocranium of a just-hatched (8·0-mm. H.-L.) young of Calotes versicolor (Daud.). 16 A, dorsal aspect. 16 B, ventral aspect. 16 C, lateral aspect. *an*, anterior naris; *aq*, articular facet of the quadrate; *bo*, basioccipital; *bpp*, basipterygoid process; *bs*, basisphenoid; *ch*, choana; *cp*, crista parotica; *cps*, cartilaginous connexion between stapes and insertion plate; *ecp*, ectopterygoid; *ep′*, epiotic portion on the posterior semicircular canal; *ep″*, epiotic portion on the anterior semicircular canal; *epi*, epipterygoid; *epl*, ligament between processus paroticus and insertion plate; *et*, egg tooth; *exo*, exoccipital; *f1*, anterior fenestra in interorbital septum; *f2* posterior fenestra in interorbital septum; *ff*, facial foramen; *fj*, foramen jugulare; *fm*, foramen magnum; *fo*, a gap in the parasphenoid; *fr*, frontal; *fro*, foramen rotundum; *hf*, hypoglossal foramina; *ip*, insertion plate of extraplectral; *ju*, jugal; *loc*, left otic capsule; *mpf*, mediopalatinal fossa; *mus*, part of stylomastoid muscle spanning crista parotica and pars superior of extraplectral; *mx*, maxilla; *na*, nasal; *oc*, occipital condyle; *of*, optic fenestra; *ope*, opisthotic part of exoccipital; *op′*, opisthotic in the posterior part of lateral semicircular canal; *op″*, opisthotic in the posterior part of posterior semicircular canal; *os*, orbitosphenoid; *pal*, palatine; *par*, parietal; *pas*, parasphenoid; *pat*, processus anterior tecti; *pc*, prominentia cochlearis; *pd*, processus dorsalis; *pfr*, postfrontal; *pi*, processus internus; *pmx*, premaxilla; *pnc*, the preoptic pillar and nasal capsule visible between the frontals; *pnl*, nasolachrymal passage; *pop*, preoptic pillar; *pp*, processus paroticus; *pr′*, prootic in the extra-otic capsule region; *pr″*, prootic in the semicircular canal region; *prf*, prefrontal; *ps*, planum supraseptale; *psc*, posterior semicircular canal; *pt*, pterygoid; *pv*, prevomer; *q*, quadrate; *r*, parasphenoidal rostrum; *roc*, right otic capsule; *soc*, sopraoccipital; *smx*, septomaxilla; *sq*, squamosal; *st*, stapes; *ste*, supratemporal; *stf*, supratemporal fossa; *uo*, unossified areas; *vc*, Vidian canal.

The epipterygoid (Text-figs. 16 A, 16 B, 16 C, *epi*) or columella cranii arises as perichondral ossification in the processus ascendens. In the adult Calotes, as in the young stage studied, the dorsal end of the epipterygoid is connected by a ligament with the ventral aspect of the parietal right in front of the supratemporal, but Narayanaswamy Iyer (1943) has described a cartilaginous connexion as in Varanus (Bahl, 1937). Ventrally the club-shaped end sits in a fossa in the pterygoid. The trigeminal ganglion is slightly posterior to the epipterygoid in the cavum epiptericum (an extracranial space), and the ophthalmicus profundus V runs medially and the other two branches of the trigeminal nerve externally to the epipterygoid.

The quadrate (Text-figs. 16 A, 16 B, 16 C, *q*) bone arises as perichondral ossification in the quadrate cartilage and is free, and, therefore, streptostylic.

The articular (see Text-fig. 5, *art*) is noticed as a circular ossification round Meckel's cartilage in the processus retroarticular region. This bone undergoes fusion with an anterior membrane bone, the prearticular. In Calotes the prearticular is present as a separate bone only in early stages.

No mento-meckelian ossification at the symphysis of the rami of lower jaw is noticed.

The ossification in the first ceratobranchial is the cornu branchiale primum.

Discussion.

In the posterior region of Calotes the basal plate shows two condyles with a notch between them and the notochord runs dorsally to the basal plate as in Lacerta (Gaupp, 1900). In early stages of Eumeces (Rice, 1920) and Sphenodon (Schauinsland, 1900) the notochord may be embedded posteriorly in cartilage; in Chelone (Gaupp, 1900) it enters the basal plate ventrally. In Emys (Kunkel, 1912) and Crocodilus (Shiino, 1914) the notochord is completely embedded.

In Lacerta (Gaupp, 1900) the intercondylar notch is not prominent, while in Eumeces (Rice, 1920) it is pronounced, and Rice homologized these condyles with the mammalian ones. In the adult Calotes the monocondyle includes the proatlas, and the condylar region shows clearly this addition. Wedged in between the exoccipital (plus opisthotic) projections, the condyle is demarcated by a thin groove on each side.

This median condyle is the hypocentrum of the proatlas vertebra, while the occipital arches represent its neural arches. The pleurocentrum of this proatlas unites with the same of the atlas and axis vertebrae to form the odontoid peg. That this happens is seen in the 3·6-mm. stage of Calotes where the occipital region of the basal plate is in temporary confluence with its own pleurocentrum (as happens normally in the vertebral region) which is already fused with the pleurocentra of atlas and axis vertebrae, the notochord projecting centrally from this. Later, a joint appears between the hypocentral condyle fused on to the basal plate between the exoccipital projections and the atlas vertebra. Thus the craniovertebral joint is intravertebral and intersegmental as in other Lacertilia (de Beer, 1937).

In Eumeces (Rice, 1920) a temporary union of the odontoid tip (pleurocentrum) with the basal plate was recorded. While in Lacertilia, Sphenodon, and Ophidia the condyle is hypocentral, the pleurocentrum forms the median condyle in Crocodilia and Chelonia.

The fissura metotica is undivided in Lacerta (Gaupp, 1900), while in Eumeces (Rice, 1920) the fissure is cut into two by the close apposition of the posterior ampullary prominence and the basal plate. The more anterior is the recessus scalae tympani lateralis, while the posterior one is the foramen jugulare for the exit of X and XI cranial nerves. Through the former the glossopharyngeal nerve comes out. In Calotes also the fissura is separated into two by the coming together of the basal plate with the prominentia ampullaris posterior with only a thin connective tissue lamella separating them, in the region of the hypoglossal foramina. The posterior jugular foramen is itself divided into an anterior larger and a posterior smaller part which transmits nothing. In the adult a part of the recessus scalae tympani lateralis becomes the fenestra rotunda, over which the secondary tympanic membrane is stretched, and through this the glossopharyngeal nerve gets out. This arrangement is as in other lizards.

The number of hypoglossal foramina varies; in Calotes there are two as in Eumeces, Platydactylus and Sphenodon (four in early stages), and later stages of Chrysemys; in Lacerta, Crocodilus, and early stages of Chrysemys there are three, and four in Tropidonotus. Rice (1920) has given a list of the number of hypoglossal foramina in various reptiles.

The septum intervestibulare divides the internal cavity of the otic capsule into an anterior smaller (cavum vestibulare anterius) and a posterior larger chamber (cavum vestibulare posterius) in lizards. In Calotes the median orifice is not limited as in Lacerta. The utriculus establishes connexion with its anterior portion by passing over the septum intervestibulare towards its dorsomedian aspect, i.e. internally to the septum semicirculare laterale (Text-fig. 15 A). This is unusual. The lateral orifice is normally situated.

In the orbitotemporal region of Calotes the formation of the interorbital septum is interesting. In the earliest stage studied (3·6 mm.) it is noticed that the preoptic roots are separate and the orbital cartilages connect each preoptic root with the pila antotica of its side (Text-fig. 1); the pila metoptica unites with the orbital cartilage in its region so that a typical fenestra metoptica is formed. In the next stage (6·0 mm.) a short interorbital septum (Text-fig. 2) has appeared which anteriorly shows forking. From the lower ends of this fork the two sphenethmoid commissures start, while from the upper the two preoptic roots proceed and meet the orbital cartilages. The two pilae metopticae connect the orbital cartilages posteriorly and there is no antotic connexion. In the 7·0-mm. stage the forked nature of the interorbital septum is lost, and, therefore, the sphenethmoid commissures diverge from the ventral end of the interorbital septum (Text-fig. 3); the two preoptic roots have united to form the planum supraseptale. An additional pillar reaching from the ventral portion of the interorbital septum to the posterior part of the planum separates an anterior septal fenestra from a posterior optic. The paired nature of the metoptic pila is lost; the taeniae mediales arising from the posteroventral border of the planum meet the united cartilago hypochiasmatica, subiculum infundibuli and pilae metopticae. In the next stage (8·0 mm.) the preoptic pillar is elongated and the ventral unpaired portion of the interorbital septum has increased in size.

In Lacerta (de Beer, 1930) the orbital cartilages do not unite with paired preoptic pillars and even in the earliest stage, (4·5 mm.) showing the planum supraseptale (which represents the anterior portion of orbital cartilages), it is single; only posteriorly by means of the taenia medialis, which represents the orbital cartilages in this region, the trabecula is connected with the paired pila metoptica. In Calotes, on the other hand, the preoptic roots are separate and these are connected with the pila antotica by the orbital cartilages to start with, and later, when the interorbital septum appears and the eyes enlarge, the preoptic roots fuse to form a pillar, the two orbital cartilages unite to form the planum supraseptale, and the posterior portion of the orbital cartilages (taenia medialis) fuse with the median pillar (united cartilago hypochiasmatica, subiculum infundibuli and pilae metopticae). The antotic connexion is lost and the taeniae marginales are also absent.

In Anguis (Zimmermann, 1913) the planum supraseptale is composed of paired separate orbital cartilages.

The fenestra metoptica in Calotes is incomplete in the 8·0-mm. stage, there being no connexion between the pila metoptica and pila antotica by a taenia medialis as in Lacerta (Gaupp, 1900). In Eumeces (Rice, 1920) also the fenestra metoptica is incomplete, the pila antotica being barely indicated.

The pila antotica ossifies, and it has been called the 'alar process' by previous workers (Siebenrock, 1892, 1894; Bahl, 1937). This is clearly the pleurosphenoid, which also becomes united with the various bones in this region of Lacerta to form an 'Os basilare commune'. In Calotes also a pleurosphenoid is noticed, but the composite sphenoid bone is separate from the basioccipital.

The ethmoid region of Calotes stands apart from other lizards described. The lamina transversalis anterior is unconnected on its lateral aspect with the roofing parietotectal cartilage, so that a zona annularis, as seen in Lacerta, is absent in Calotes.

The nasolachrymal duct, however, opens into the choanal region behind the lamina transversalis anterior, which is also the condition in Lacerta (Gaupp, 1900).

The lamina orbitonasalis unites with the anterior portion of paranasal cartilage in Calotes, and a concha nasalis, so characteristically seen in lizards, is absent in Calotes. In this it resembles Sphenodon. Further, no lateral fenestra is seen in Calotes, and in the side view the nasal septum and ectochoanal cartilages are seen (Text-fig. 14 c). The lateral nasal glands are accommodated in a space—the cavum conchale, between the posterior portions of the paranasal and parietotectal cartilages; in other lizards the glands are enclosed in a cartilaginous concha nasalis.

Starting from the median aspect of the lamina transversalis anterior and meeting the median wall of the lamina orbitonasalis is the paranasal cartilage in Lacerta, which is unconnected with the nasal septum. In Calotes this cartilage is wanting; there is only a short projection from the median aspect of lamina orbitonasalis.

The lamina orbitonasalis is demarcated from the nasal capsule by the epiphaneal foramen and the processus maxillaris anterior is seen anterolaterally from the lamina. While a posterior maxillary process is not visible in the 8·0-mm. stage embryo, in the young of Calotes of the same head-length two cartilaginous parallel projections run dorsally to the palatine from the lamina orbitonasalis. The more ventral of these is the processus maxillaris posterior while the other is without significance. In Lacerta (Gaupp, 1906), also, on the dorsal aspect of the palatine, isolated nodules of cartilage in line with the processus maxillaris posterior are recorded.

In Calotes, on the posterior aspect of the lamina orbitonasalis, on each side of the interorbital septum, there is a small cartilaginous projection, and I have called it the posterior laminal process.

The pterygoquadrate (Text-fig. 11) is represented as a separate movable quadrate posteriorly, a processus ascendens (which ossifies into the epipterygoid) and a basal process (the meniscus pterygoideus; the metapterygoid of fishes) articulating with the basitrabecular process; no processus pterygoideus is noticed. However, in earlier stages, from the region where later the processus ascendens appears, there is an anteriorly directed mesenchymatous strand representing the processus pterygoideus. This does not chondrify. In Lacerta there is a processus pterygoideus united with the processus ascendens, which is always separate from the quadrate, and in Eumeces (Rice, 1920) the processus pterygoideus is independent of the processus ascendens; in earlier stages of Eumeces the processus ascendens and processus pterygoideus and quadrate are united. In Mabuia, Zonurus, and Eremias (Broom, 1903) there is a persistent cartilaginous connexion between quadrate and epipterygoid. In Sphenodon (Howes and Swinnerton, 1901), Chrysemys (Shaner, 1926), and crocodile (Parker, 1883) these processes are united with the quadrate cartilage. According to Fürbringer (1904), to ensure greater mobility of the jaw, the quadrate becomes separated off from its anterior connexions. Characteristically the quadrate of the snake is also free from all these processes.

The columella auris shows, in the young Calotes with the head-length of 8·0 mm., an ossified stapes and a cartilaginous extracolumella. From the insertion plate which fits into the tympanic membrane there arise the characteristic processes: the pars inferior and pars superior. From the latter arise the processus accessorius anterior and posterior. Arising from the pars superior there is a ligament passing into the processus paroticus and a muscle which is a part of the stylomastoid muscle inserted on the crista parotica.

From the processus accessorius anterior there is a ligament attaching itself to the quadrate; such a structure is also described in some chelonians by Fuchs. From the connecting cartilaginous piece between the insertion plate and stapes in Calotes there arises the processus internus which articulates with the quadrate and a ligamentary processus dorsalis which meets the processus paroticus.

The processus accessorius anterior connexion with the quadrate is not noticed in Lacerta (Gaupp, 1900) and Eumeces (Rice, 1920).

Generally the processus accessorius posterior or processus interhyalis unites with the ceratohyal in early stages and this connexion may even persist in later stages. In early stages of Lacerta (Hoffmann, 1889; Gaupp, 1900), Eumeces (Rice, 1920), Tropidonotus (Rathke, 1830), and Crocodilus (Parker, 1883) the connexion is noticed. In Sphenodon (Howes and Swinnerton, 1901) the connexion is permanent. There may be a mesenchymatous connexion between the pars interhyalis and ceratohyal in Chelonia (Bender, 1911; Smith, 1914); in Emys (Kunkel, 1912), however, there is a ligament running between the pars interhyalis and the retroarticular process of the lower jaw.

A processus dorsalis is noticed in Lacerta (ligamentary, Gaupp, 1900) and Calotes. In Eumeces (Rice, 1920) and Lygodactylus (Brock, 1932) it is absent. In Agama (Brock, 1932) it persists as a cartilaginous connexion. In Varanus, topographically, a ligamentary processus dorsalis is present, though Bahl (1937) noted to the contrary. In Sphenodon (Howes and Swinnerton, 1901; Versluys, 1903) the dorsal process is united with the quadrate; in Tropidonotus an independent chondrification acquiring connexion with the quadrate is homologized with the processus dorsalis (de Beer, 1937). While it is absent in Chelonia (Kunkel, 1912), in Crocodilus it fuses with the quadrate.

A cartilaginous processus internus projects towards the quadrate in Calotes, and as in Lacerta (Gaupp, 1900) there is no union with the quadrate (see, however, de Beer, 1937, p. 225). In Eumeces (Rice, 1920) it is very short and in Lygodactylus (Brock, 1932) it is absent. So also in Sphenodon (Howes and Swinnerton, 1901), Tropidonotus (Parker, 1879), Emys (Kunkel, 1912), and Crocodilus (Goldby, 1925).

The last ligamentary connexion is the one that starts from the pars superior of the insertion plate and gets inserted on the processus paroticus at the region where the processus dorsalis ligament also meets it in Calotes. The chorda tympani runs dorsolaterally to this ligament, while the stapedial artery runs medially to the processus dorsalis. In describing this tendon, Rice (1920) recorded its presence in Eumeces (with the chorda tympani running dorsally to it) and noted: 'This "tendon of extracolumella" is carefully described by Versluys (1898) for Sphenodon and adult lizards; it was only lacking in Amphisbaena among the many lizards studied.' In Varanus Bahl (1937) described it running into the crista parotica, but the chorda tympani had no relation either with the processus dorsalis ligament or this. Probably on account of this, he denied the presence of a processus dorsalis. In Agama (Brock, 1932) there is the extracolumella-crista ligament, but the chorda tympani does not loop round it. All the same Brock noted: 'From the condition in Lygodactylus where there is a cartilaginous connexion between the extracolumella and the crista parotica in early stages it may be judged that the ligament of Agama, Lacerta, etc., is homologous with the cartilaginous and ligamentous connexion of the Geckos and the latter would then be the more primitive condition.' In all the examples (see below) where such a ligamentary or cartilaginous (laterohyal) connexion is noticed, the chorda tympani always runs dorsolaterally to it; while the ligamentous connexion of Calotes and Eumeces may be homologous with the laterohyal, that of Agama and Varanus must be considered analogous.

In Sphenodon, from the processus paroticus or intercalary there is a laterohyal cartilage uniting with the extracolumella enclosing a 'Huxley's' foramen between the processus dorsalis and the laterohyal; the chorda tympani runs laterally to it. There is in addition to this a ligament from the extracolumella to the crista parotica and the exact homology of this tendon when there is a permanent laterohyal connexion with the ceratohyal becomes difficult, and Versluys assumed that the connexion of the hyoid arch has been secondarily regained. A similar laterohyal connects in Crocodilus (Versluys, 1903) the intercalary with the epihyal, which itself is in contact with the extracolumella by means of the pars interhyalis; the chorda tympani runs laterally to the laterohyal (de Beer, 1937, Pl. 141, fig. 17).

In Geckos with the ligamentary connexion between the extracolumella and parotic process (which may be cartilaginous in early stages, e.g. *Lygodactylus* (Brock, 1932, fig. 6 B)) the ceratohyal is directly connected with the parotic process, with the chorda tympani bearing no relation to it (or by-passing laterally to it, de Beer, 1937, Pl. 141, fig. 13), apparently resembling a laterohyal. However, in early stages the extracolumella is connected both with the processus paroticus and ceratohyal.

A brief reference may be made to the muscle that arises from the pars superior and gets inserted on the crista parotica. Externally to the ligament referred to above, the muscle has been noticed in *Lygodactylus* also (Brock, 1932). It is noted by the author that the muscle is a part of the stylomastoid and not depressor mandibulae as Versluys would have it. Having examined early and late stages of *Calotes*, I am in agreement with Brock.

Summary

1. In the earliest stage of *Calotes* studied, the basal plate is confluent with the pleurocentrum of the atlas and axis vertebrae. Later, a joint appears between the hypocentral condyle and the first vertebra. This shows that, at least temporarily, the elements of the anterior sclerotomic half in this region are in continuity with the posterior in front as happens in the vertebral region. The occipito-atlantic joint is, therefore, intravertebral and intersegmental as in other Lacertilia.

2. The anterior semicircular canal is completely separated for a short distance from the remaining otic capsule. The gap is filled with connective tissue.

3. The intervestibular septum shows a lateral foramen which transmits nothing and the utricular connexion between the anterior and posterior chambers passes posteriorly to the median part of the septum and, therefore, a medial orifice is not formed.

4. The preoptic roots, the orbital cartilages, and metoptic pila are paired in early stages; the orbital cartilage connects the

preoptic root, pila metoptica and pila antotica dorsally. Later the two preoptic roots merge to form a median preoptic pillar, the orbital cartilages anteriorly unite to form the planum supraseptale, while posteriorly also the orbital cartilages (taenia medialis) unite at the region of the hypophysial foramen. This posterior united portion is met by a median vertical pillar (formed by the fusion of cartilago hypochiasmatica, subiculum infundibuli, and pilae metopticae) arising from the trabecula communis.

The single septal fenestra is divided into an anterior larger and a posterior optic by the formation of median interorbital pillar from the ventral interorbital septum which meets the posterior portion of the planum supraseptale. The ventral portion of the interorbital septum is never noticed to be paired; the taenia marginalis is absent. However, short projections from the posterodorsal margin of the planum and from the anterodorsal face of the otic capsule represent the reminiscence of marginalis connexion. A supratrabecular bar is absent.

5. In the nasal capsule, a concha nasalis is absent; therefore, the lateral nasal glands are unenclosed in a cartilaginous capsule. The anterior portion of the paranasal cartilage unites with the dorsal portion of the lamina transversalis anterior, and the latter gives rise to an ectochoanal cartilage, but a paraseptal cartilage is absent. On the ventral side, from the free median margin of the lamina orbitonasalis, there arises a short projection which represents the posterior portion of the paraseptal cartilage.

6. The pterygoquadrate shows a free streptostylic quadrate, a processus ascendens which ossifies into the epipterygoid, a processus pterygoideus only in early stages, a basipterygoid articulation by a free meniscus cartilage, and an otic articulation with the crista parotica and processus paroticus by the quadrate.

7. The columella auris shows a ligamentary processus dorsalis connexion with the processus paroticus, a cartilaginous processus internus which articulates with the quadrate, a processus accessorius anterior which is connected with the quadrate by a ligament, and a ligamentary connexion between the pars superior of the insertion plate and processus paroticus. The

processus accessorius posterior-ceratohyal connexion was not noticed. There is also a muscle (a part of M. stylohyoid) spanning the pars superior and crista parotica. The pars superior-paroticus ligamentary connexion, with the chorda tympani running laterally to it, is homologized with the laterohyal of Sphenodon and the crocodile.

8. The hyoid apparatus shows a processus lingualis and cornuhyale (paired hypo- and ceratohyals) arising from a median basihyal and two pairs of ceratobranchials.

9. In the osteocranium, the oto-occipital of each side is formed by the fusion of opisthotic and exoccipital, while the supraoccipital is formed by an ossification in the tectum and its fusion with the two epiotics formed in the sinus region of the otic capsule. The basioccipital and the composite 'sphenoid' are not united. The pleurosphenoid ossifies in the pila antotica. The epipterygoid is connected at its dorsal end with the parietal by a ligament, and ventromedially it is free from the meniscus cartilage. The frontals and parietals are paired in the stage examined, and in the adult the parietals of each side fuse, as also the frontals.

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